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Effects of Excessive Nitrogen Deposition on Foliar Nutrient Dynamics, Nutrient Concentrations, and Nutrient Ratios in a Central Appalachian Hardwood Forest

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ABSTRACT

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Many forested systems of the eastern US are becoming significantly nitrogen (N) saturated due to chronic N deposition from the atmosphere. Nitrogen saturation has the potential to alter important internal plant processes, such as nutrient cycling. While extensive research has been conducted on the responses of soil to N saturation, considerably less research has focused on the response of plant nutrient dynamics, nutrient concentrations, and nutrient ratios to excess N. Research was conducted on two watersheds at the Fernow Experimental Forest in West Virginia: WS3 (fertilized with ammonium sulfate annually since 1989) and WS7 (untreated control). Presenescent and senesced leaves were collected from *Liriodendron tulipifera* L., *Prunus serotina* Ehrh., and *Acer rubrum* L. on each watershed and analyzed for N, P, Al, Ca, and Mg content. In addition to nutrient concentration and ratio analyses, the rates of both N and P resorption were also determined. Results were highly variable between species and between watersheds. Initially, N and P concentrations were much higher on WS3 than WS7, however, by 2000 these differences were no longer significant. Overall, Al concentrations increased and Ca/Mg concentrations decreased in response to increasing N concentrations. Despite variations among species, the results indicate that WS7 may be moving towards a condition similar to that of WS3 at the start of treatment or towards N saturation. The ratios of Ca:Al were found to be considerably lower in LITU on both WS3 and WS7, which may be indicative of decline of the species. Values for both N and P resorption were higher on WS7 with values ranging from 69.5-82.4% for P and 74-81% for N. These results strengthen previous findings that plants on nutrient poor sites are more efficient at resorption. The complexity of interactions

involved in internal plant processes, coupled with the detrimental effects of N saturation, merits further research to gain better understanding of how excess N deposition affects not only forested watersheds, but also entire forested ecosystems.

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Ah, a reprieve from toiling over the thesis! Most people probably save this part for last, waiting until the main product is all shiny from constant polishing. However, I've never been most people, and I need a break! So on to the easy and fun part of the whole deal, reflecting about the years past and giving credit where credit is due!

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Chapter I. Introduction

Nitrogen Saturation

The biogeochemical cycles of the Earth have been greatly altered by human activities, with a major component of this impact being caused by the burning of fossil fuels. Combustion of coal, gasoline, and oil increases both the pollution concentrations in the atmosphere and the deposition rates of pollutants to the surface (Aber et al. 1989). One important phenomenon associated with such increases in pollution levels is acidic deposition. The main focus of regulations on acidic deposition in the United States has been sulfur emissions and the sulfuric acid deposition component (Aber et al. 1989). The Clean Air Act (1970) contained provisions that targeted sulfur emissions; however, no limits were placed on the emission of nitrogenous compounds. Although emissions of sulfur decreased by approximately 25% during the twenty years following the legislation, emissions of nitrogen (N) increased by 2% (Gilliam and Adams 1999). Despite this increase in N input, the 1990 Amendment to the Clean Air Act only called for a 10% reduction in nitrogen emissions, while again placing higher limits on sulfur - this time with a reduction goal of 50% (Schaberg et al. 1997).

Now, increasing concern over the N component of pollution and its possible effects on air quality, water quality, and health of forest ecosystems is mounting. Atmospheric nitrogen deposition in the United States is currently 10-20 times above historic background levels (Magill et al. 1997), with deposition rates expected to increase by 25% over the next 25 years (Adams 1999). Rates of N addition to forest ecosystems through wet and dry atmospheric deposition range from less than 2 kg N/ha/yr in areas largely unaffected by industrial sources, to more than 40 kg N/ha/yr at high elevations in New England (Aber et al. 1989). The largest sources of nitrogen oxides are the urban centers along the east coast, the industrialized regions of the Great Lakes, and the Ohio River Valley (Lovett and Rueth 1999).

Since most forest ecosystems in humid, temperate climates were traditionally considered to be N limited, concerns have arisen regarding their ability to absorb and accumulate excess N (Aber et al. 1989, Magill et al. 1997). Nitrogen limitation occurs

because external inputs, whether from atmospheric deposition or biological fixation, are lower than the nutritional demand or uptake potential of plants (Asner et al. 1997). Plants must meet most of their nitrogen requirements by efficiently recycling nutrients between living plant tissues and decomposing organic matter. When nitrogen is limiting in such systems, this recycling results in low losses to the environment (Asner et al. 1997). However, excess N availability in such systems places a unique stress on plants which are not suited to such conditions and may lead to toxic effects and nutrient imbalances (McNulty et al. 1990). While N deposition at low rates may produce a fertilizer effect in N deficient sites by increasing the proportion of N taken up by plants and by stimulating growth, the potential for forest ecosystems to incorporate and retain all added N is limited (Aber 1992). The long-term removal of N limitations on biotic activity, accompanied by a decrease in N retention capacity, has been termed nitrogen saturation (Magill et al. 1996).

Nitrogen saturation is defined as the availability of ammonium and nitrate in excess of total combined plant and microbial nutritional demand (Aber et al. 1989). Excess N in watersheds is detrimental because of disruptions in plant/soil nutrient relations, such as increased nitrate (NO_3^-) leaching and simultaneous base cation losses (Magill et al. 1997). Other symptoms include increasing N concentrations and higher N:nutrient ratios in foliage (e.g., N:Mg, N:P), foliar accumulation of amino acids or NO_3^-, increased soil acidification and Al mobility, and decreased water quality (Fenn et al. 1998). Some forests receiving chronic N inputs may decline in productivity and experience greater mortality (Fenn et al. 1998).

The response of a forest ecosystem to such elevated inputs of N involves a complex interaction among processes affecting N cycling. Such processes include: deposition, plant uptake and allocation, litter production, immobilization and mineralization during litter and soil organic matter decay, nitrification, ion leaching, and trace gas emissions (Aber et al. 1989). Four stages involving the process of N saturation have been defined. Stage 0 is representative of a forest under normal conditions where N is still limited within the system. Stage 1 represents a forest experiencing the initial effects of chronic N deposition, such as elevated foliar N content and increased growth. Stage 2 represents a forest when N saturation levels have been

reached and Stage 3 represents forest decline under N saturated conditions (Aber et al. 1989).

Many areas of temperate forest in the northeastern United States are becoming increasingly N saturated due to chronic atmospheric deposition, with some of the highest levels occurring in Ohio, Pennsylvania, New York, western Maryland, and northern West Virginia (Aber et al. 1989, Peterjohn et al. 1996). The large number of urban watersheds located in the northeastern and central United States account for the large inputs of N to the region (Fenn et al. 1998). In general, the deposition of N decreases along a southwest-to-northeast gradient, due to the depletion of nitrogen oxides from air masses as they move downwind from source areas (Ollinger et al. 1993). It has also been found that geographic patterns of N deposition follow patterns of N loss from watersheds in the northeastern United States. The greatest amount of N deposition and watershed loss of N occurs in the Adirondack and Catskill Mountains of New York, with little watershed loss of N occurring in Maine, where N deposition is approximately 50% lower (Fenn et al. 1998).

In addition to the high elevation spruce-fir forests of the Northeast and the hardwood forests of the central Appalachian region, the mixed coniferous forests of southern California and the high elevation catchements in the Rocky Mountains represent other areas in the United States where N saturation is well documented (Adams 1999). Dry deposition of N in the Los Angeles Air Basin is among the highest in North America (Fenn et al. 1996). It is also well documented that European forests receiving elevated levels of N deposition are exhibiting several symptoms of nitrogen saturation (Peterjohn et al. 1996).

The potential for N saturation in the hardwood forests of southern and central Appalachia is particularly high due to increased levels of N deposition in the area. Studies conducted in the 1980s demonstrated that high elevation southern Appalachian spruce-fir forests received among the highest levels of N measured in North America (Nodvin et al. 1995). Wetfall inputs of N can be greater than 10 kg N/ha/yr and total N deposition may be as much as 4-5 kg N/ha/yr higher than wetfall amounts when dry deposition of N is included (Gilliam et al. 1996). Most research in the area has been directed at spruce-fir forests because of an observed dramatic decline and public

concern over the issue (Gilliam and Adams 1996). However, considerably less research has concentrated on the effects of such deposition on hardwood deciduous species even though they dominate most of the forests in this region. Hardwood leaves are most susceptible to pollution damage during rapid springtime growth; therefore, seasonal patterns of acid precipitation may be more meaningful than annual averages in assessing the potential impact on hardwood forests (Gilliam and Adams 1996).

Recent data indicate that several eastern deciduous forest species are experiencing higher than normal rates of decline (Gilliam and Adams 1999). Despite debate, the observed mortality has been attributed to a variety of factors including acidic deposition, nutrient cation depletion, and nitrogen deposition. All factors, alone or cumulative, have the ability to decrease the survivorship of several forest species by weakening the trees and increasing their vulnerability to other stresses, including temperature and moisture extremes, disease, and insects (Gilliam and Adams 1999).

Foliar Nutrient Dynamics

Leaf senescence plays a vital role in plant fitness due to reclamation of nutrients for future use. During senescence, chlorophyll is broken down by chemical processes and nutrients are then withdrawn into perennial tissues for storage in a process called resorption (Ryan and Bormann 1982; Killingbeck et al. 1990). Resorption is defined as the mobilization and removal of substances from senescing plant tissues and the subsequent transportation of these substances to surviving tissues (Killingbeck et al. 1990). Decreases in the absolute amounts of N, P, or K are also recognized during senescence (Ryan and Bormann 1982). Resorption, storage, and remobilization allow trees to be relatively independent of soil supplies of critical nutrients during short periods of high demand, such as the springtime growth period (Ryan and Bormann 1982). Also, resorption and remobilization may promote more uniform growth from year to year by linking current growth to conditions that prevailed in previous years (Ryan and Bormann 1982). Timing of resorption, such as that during the autumn, as opposed to summer, may also contribute more to storage and to the subsequent remobilization of N the following spring (Tagliavini et al. 1999).

Nutrient resorption is a phenomenon in all forest trees (Ryan and Bormann 1982) and is one of the most important strategies employed by plants to conserve nutrients and therefore influence processes such as competition, nutrient uptake, and productivity (Killingbeck 1996). Transfer of nutrients from leaves to woody tissues within the tree reduces the likelihood of nutrient loss through water movement or by litter removal (Ostman and Weaver 1982). Rainfall, especially that which is acidic, can leach nutrients from foliage (Ryan and Bormann 1982) and make elements which are toxic to plants (i.e., Al) readily available for uptake. They also break down barrier systems which inhibit the transfer of such elements inside plants (Gjengedal 1996). Even minor pH changes associated with increased deposition levels can increase Al availability and reduce the retention time of nutrients such as Ca and Mg (Gjengedal 1996). The breakpoint for the effects of acid on foliage was found to be approximately pH 3.0 in both in situ and laboratory studies (Gjengedal 1996).

Resorption may be important on any nutrient-poor site or whenever external nutrient recycling is interrupted (Ostman and Weaver 1982). Killingbeck (1996) found that resorption is highly proficient in plants that have reduced nitrogen and phosphorus concentrations in their senescing leaves to below 0.7% and 0.05%, respectively. Some studies comparing nutrient losses from plants on nutritionally distinct sites suggest that plants growing on infertile soils may minimize nutrient loss by resorbing a greater fraction of N and P from senescing leaves (Stachurski and Zimka 1975). However, other studies (Chapin and Kedrowski 1983) have demonstrated that the nutrient use efficiency of species growing on nutrient rich substrates exceeds that of species growing on infertile substrates. Although conflicting studies exist regarding site fertility and its relationship to nutrient resorption efficiency, it is apparent that resorption efficiency varies considerably among species.

During autumnal senescence, plants generally resorb about half of the total N and P that was originally invested in leaves; however, this resorption efficiency varies from 0 to 90% depending on habitat and species (Chapin and Moilanen 1991). Individual plants and plant populations can resorb markedly different amounts of nutrients in different years (Killingbeck 1996). Seasonal availability and extent of nutrient transport from the soil also affect resorption values (Gjengedal 1996). In

deciduous species, resorption augments the reservoir of nutrients available to support metabolic activity in subsequent growth periods (May and Killingbeck 1992). It is estimated that in a southern Appalachian deciduous forest, 34.6 kg N/ha/yr were “cycled internally” by trees and provided 22% of the forest’s annual N requirement (Ryan and Bormann 1982).

While extensive research has been conducted regarding soil responses to N saturation, relatively little research has focused on the effects of N saturation on foliar nutrient dynamics. The internal cycling of nutrients is an important and complex mechanism that allows plants to conserve and to maintain needed quantities of nutrients, particularly N and P. Determining the effects of N saturation on foliar nutrient dynamics at the watershed level will allow a better understanding of such effects on entire forest ecosystems. This thesis research was part of a two-year seed grant study in which the effects of N saturation on foliar nutrient concentrations, resorption efficiencies, and foliar nutrient ratios were examined. Future research may examine the effects of nitrogen saturation on processes within plant systems, especially the differences that exist between species.

Chapter II. Material and Methods

Study Site

The Fernow Experimental Forest (FEF) was established in 1934, on land set aside in the Monongahela National Forest for use in sustainable forest management research. It is currently maintained by the USDA Northeastern Forest Service Timber and Watershed Laboratory in Parsons, WV. The main focus of research at FEF is on the maintenance of both the productivity and the diversity of soil, water, and forest resources within central Appalachian forests.

Fernow Experimental Forest is located near Parsons, West Virginia (Tucker County) and occupies approximately 1900 hectares of the Allegheny Mountain section of the unglaciated Allegheny Plateau (Fig. 1). Mean monthly air temperatures range from -1°C to 5°C in January, to 25°C in July; winter lows occasionally range from -20°C to -10°C and summer highs range from 30°C to 35°C. Mean annual air temperature for the site is approximately 9°C (Adams et al. 1994).

Average precipitation at the site is 1430 mm/yr, with the highest levels of precipitation being received during the growing season and at higher elevations (Gilliam et al. 1995). Snowfall averages 1370 mm/yr, with most falling during January and February. However, due to low water content, snowfall contributes only about 14% to overall yearly precipitation (Adams et al. 1994). Average annual pH of precipitation is approximately 4.20, with mean values ranging from 4.12 – 4.31 and seasonal means as low as 3.99 (Adams et al. 1994).

Soils of the area are Calvin channery silt loam (loamy-skeletal, mixed mesic Typic Dystrochrept) underlain with fractured sandstone and shale of the Hampshire formation (Adams et al. 1995) and are generally less than one meter in depth (Gilliam et al. 1995). All watersheds are drained by second-order streams.

The watersheds used in this study, Watershed 3 (WS3, experimental) and Watershed 7 (WS7, control) are adjacent to one another and typical of second growth hardwood forests of this region prior to treatment. Both watersheds support tree stands of similar age (~ 30 yrs) and are characterized by steep slopes and shallow soils.

Dominant canopy species include sugar maple (*Acer saccharum* Marsh.), red oak (*Quercus rubra* L.), yellow poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), and black birch (*Betula lenta* L.). The herbaceous layer is heterogeneous, with species of violet (*Viola* spp.) and stinging nettle (*Laportea canadensis* (L.) Wedd.) dominating WS3 and several species of fern, including marginal shield fern (*Dryopteris marginalis* L. Gray) and Christmas fern (*Polystichum acrostichoides* Michx. Schott.), dominating WS7 (Gilliam et al. 1996).

Watershed 3 occupies 34.27 ha and ranges in elevation from 735-860 m with a southern aspect (Figs. 2-3). Trees >12.7 cm in diameter at breast height (dbh) were selectively cut from 1958 to 1959 and again in 1963. In 1970, WS3 was clearcut to 2.5 cm dbh and has received three yearly applications of granular $(NH_4)_2SO_4$ since 1989. March and November applications equal 33.6 kg/ha (or 7.1 kg N/ha and 8.1 kg S/ha) and the July application equals 100.8 kg/ ha (or 21.2 kg N/ha and 24.4 kg S/ha) (Gilliam et al. 1996). These rates are approximately two times the ambient rate of nitrogen deposited annually.

Watershed 7 has a total area of 24.23 ha, with elevation ranging from 725-855 m and an eastern aspect (Figs.4-5). Between 1963 and 1964, the upper 12 ha of the watershed were clearcut, then from 1966 to 1967 the lower 12 ha were cut (Gilliam et al. 1995). Prior to release, from 1964-1969, WS7 was maintained barren with herbicides and has received no treatments since.

Sampling Methods

Three individuals each of red maple (*Acer rubrum* L.), tulip poplar (*Liriodendron tulipifera* L.), and black cherry (*Prunus serotina* Ehrh.) were sampled on each watershed in the late summer and late fall of 1999 and 2000. Presenescent leaves were shot from tree crowns using a 12-gauge shotgun and a #2 or #4 stainless steel shot. Senesced leaves were collected between early October and early November from beneath selected trees. Latex gloves were worn during collection of leaves and during analysis whenever leaf samples were handled to minimize contamination.

Laboratory Analysis

Surface areas of all leaves were measured using a LI-COR model LI-3100 area meter. Leaves were oven-dried at 60 ºC for 48 hours, weighed, and ground in a Wiley mill to pass through a 40-mesh screen. Total N and phosphate P were extracted using

an EPA Kjeldahl block digestion procedure (EPA Method # 351.2). Digested samples were analyzed for total N and P concentrations using a Bran+Luebbe Traacs 2000 continuous flow analyzer. Additional samples were ashed at 500 ºC, dissolved in nitric acid, and analyzed for Al, Ca, K, and Mg concentrations using a Varian Liberty 110 ICP Emission Spectrometer.

Statistical Analysis

Due to the amount of sampling at FEF, sample size was limited to three individuals of each species; this should be considered when interpreting statistical data. Differences among species and between watersheds were determined using t-tests at a significance level of $p<0.10$. A significance level of $p<0.05$ was considered to be highly significant, while values ranging between $0.10>p>0.05$ were considered to be marginally significant. Graphs were generated using STASTITICA software. All 1992 data used for comparative analyses were provided by Dr. Mary Beth Adams, project coordinator, USDA Timber and Watershed Laboratory, Parsons, WV.

RESULTS AND DISCUSSION

Chapter III. Nutrient Concentrations in Green Foliage

Foliar Nitrogen and Phosphorus Concentrations

In 1992, three years after initiation of ammonium sulfate additions, several trends were evident in foliar nutrient concentrations of green foliage, some of which are consistent with patterns of N saturation. Elevated concentrations of foliar N were predicted to be characteristic of a N saturated forest system (Aber et al. 1992), and other studies have since proven that increased foliar N and N to nutrient ratios are nearly universal phenomena in all N-saturated forests (Fenn et al. 1998). All three species on WS3 exhibited higher N and P levels compared to WS7 in 1992 (Figs. 6A and 6B).

Nitrogen and phosphorus concentrations were similar in their yearly patterns for LITU and PRSE (Fig. 7 & Fig. 8). Nitrogen concentrations on WS3 were significantly higher in both ACRU and PRSE in 1992 (Table 1). By 2000, these differences were non-existent, however, values of N for ACRU on WS7 increased (Table 1). The concentration of N in ACRU decreased significantly on both watersheds between 1992 and 2000 (Fig. 7, Table 2). From 1999 to 2000, N concentrations increased significantly in LITU and PRSE on WS3 (Fig. 7). In 1992, concentrations of P were significantly higher on WS3 in all three species, however by 2000, differences between watersheds were no longer significant (Fig. 8, Table 1). Values of P decreased significantly in ACRU on WS3 from 1992 to 2000, while increasing in PRSE on both WS3 and WS7. Phosphorus concentrations increased significantly in LITU on WS3 between 1999 and 2000 (Table 2). Phosphorus also increased significantly in PRSE on WS3 and marginally on WS7.

By 2000, however, there were hardly any differences between watersheds, despite the fertilization treatment received on WS3. Comparisons between 1992 and 2000 data show that N concentrations actually decreased on WS3, while increasing on WS7. This indicates that not only is WS7 becoming N-saturated, but also that luxury consumption in the presence of excess N may only be temporary.

Increased concentrations of N were expected, as other studies involving N fertilization show the same results (Boerner 1984; Aber et al. 1993; Adams et al. 1995;

Pickens et al. 1995; Magill et al. 1997). Treated larch at FEF exhibited significantly greater foliar N (2.3 %) as compared to the control (2.13%) in a study by Pickens et al. (1995). Nitrogen treatments at the Harvard Forest, Petersham, Massachusetts, also resulted in significant increases in foliar N concentrations with mean foliar N on the two highest N treatments being at least 40% higher than reported for mature spruce in New England (Schaberg et al. 1997). Chronic N additions at Harvard Forest and high N treatments have resulted in considerable alterations of the N cycle in both pine and hardwood stands (Magill et al. 1997).

Higher N concentrations result in increased N cycling rates as more N is returned to the forest floor in litterfall (Magill et al. 1997). If nitrate is not taken up by plants or incorporated by the microbial population, it will leach from the soil accompanied by base cations (Magill et al. 1997). Removal of these nutrients and their replacement with hydrogen would lead to a reduction in soil nutrient status and reduced plant growth, despite the availability of added N (Magill et al. 1997). An aggrading forest will more readily take up additional N inputs compared to a steady-state forest with slower growth and lower nutrient requirements (Magill et al. 1997).

At the Harvard Forest, in response to three years of chronic N fertilization, green foliar N increased over time in the pine stand. Also, foliar N concentrations increased by 19% in red maple and by 6% in black oak on the high N plot as compared to the control (Aber et al. 1993). By the 6th year of treatment, the percentage of N in black oak, red maple, and black birch foliage averaged 25% higher in the high N plot than in controls (Magill et al. 1996; Magill et al. 1997). Nitrogen limitation on biological activities was stronger in the hardwood stand than in the pine before treatment and pine is progressing more rapidly toward a nitrogen saturated condition (Aber et al. 1993). Data support the concept of highly nonlinear responses of nitrate leaching to chronic additions of N and N-limited forests (Aber et al. 1993). This nonlinearity results from the need to “saturate” biological demands for nitrogen before nitrification and N loss begin and varies depending on the internal state of the system (Aber et al. 1993).

Increased growth has been observed over several years following a single application of N fertilizer in pin cherry and other tree species and the averaging effect might be a factor in prolonged responses of woody plants to temporarily high nutrient

availability (Ryan and Bormann 1982). Further investigation is needed to determine if and how plants respond to chronic additions of N from the atmosphere. Rather than creating an averaging effect over several years after a treatment, continuous additions of N may produce a cumulative effect and have the potential to cause disruptions in plant processes over time.

It has also been found that some species show different responses to the form of nitrogen they receive, either ammonium or nitrate (Crabtree and Bazzaz 1993). Gray, white, and black birch all showed significantly greater growth in response to 50 kg/ha/yr nitrate treatments and gray birch responded to 50 kg/ha/yr ammonium addition. Under N deposition regimes that increase soil nitrate availability, responses of species to various N forms may ultimately lead to species composition changes (Crabtree and Bazzaz 1993). More research is therefore needed to determine if other species respond differently to the various forms of nitrogen and if so, how this may lead to alterations in composition of forests that are N saturated or have the potential to become N saturated.

Foliar Aluminum Concentrations

In ACRU, the concentration of Al was lower on WS3 than on WS7; however, both LITU and PRSE exhibited higher Al concentrations on WS3 (Fig. 9). By 2000, various changes existed in the relationships between the nutrient concentrations. Concentrations of Al were found to be marginally lower on WS3 in ACRU and significantly higher in LITU on WS3 in 1992 (Fig. 10, Table 1). By 2000, only Al concentrations in PRSE on WS7 were found to be marginally higher (Fig. 10, Table 1). Aluminum concentrations were lower in ACRU on both WS3 and WS7 from 1992 to 2000. From 1999 to 2000, no significant differences existed between watersheds for any of the three species; however, concentrations of Al increased in LITU on both watersheds.

Aluminum toxicity is widely considered an important growth limiting factor for plants in strongly acidic soils (Kidd and Proctor 2000). Tree species exhibit variable sensitivity to Al and exposure to Al may lead to declines in tree health and changes in species composition (Lux and Cumming 1999). As soil systems become acidified due

to elevated N and other atmospheric inputs, Al is increasingly mobilized in the soil solution (Lux and Cumming 1999). Lux and Cumming (1999) found that LITU seedlings show considerable sensitivity to Al even at low concentrations. However, it is not evident if mature LITU trees exhibit the same degree of sensitivity to Al.

Pickens et al. (1995) found that N-fertilized larch had significantly greater Al levels and significantly lower P and Mg levels as compared to the control. Lower foliar P in treated larch may be due to the formation of an Al-PO_4 precipitate, possible contributing to lower P availability and the lower the availability of soil P, the more quickly this antagonism develops with added N (Pickens et al. 1995). After applying treatments of ammonium sulfate over 5 years, 8 months and 6 years, 8 months, the larch on WS9 had reduced height and diameter growth compared to the control trees (Pickens et al. 1995).

Foliar Calcium and Magnesium Concentrations

Calcium and magnesium concentrations were significantly lower in all three species on WS3 in 1992 (Fig. 11 A,B; Table 1). The concentration of Ca increased marginally in both ACRU and PRSE on WS3 from 1992 to 2000 and increased significantly in LITU (Fig. 12, Table 2). The differences in Mg concentrations between watersheds for ACRU and PRSE were slightly significant (Fig. 13, Table 1). By 2000, the differences between watersheds were no longer significant. However, the difference in Mg concentrations between 1992 and 2000 were significantly lower in ACRU on both WS3 and WS7 and in LITU on WS7 (Table 2). From 1999 to 2000, differences between years were not found to be significant for Ca or Mg concentrations.

Lower Ca concentrations in LITU in our study could be a result of higher Al concentrations on WS7, since Al has a negative influence on Ca translocation to foliage (Lux and Cumming 1999). LITU has a high Ca requirement in contrast to other deciduous tree species and the restriction of Ca translocation to foliage by Al toxicity makes it especially detrimental to the species (Lux and Cumming 1999). Increased nitrate mobility in soils increases cation leaching losses and soil acidification (Gilliam et al. 1996; Aber et al. 1998). Upon acidification, significant increases in Al concentrations are observed throughout the growing season, along with increases in foliar leaching of

both Ca and Mg (Gjengedal 1996). However, Ca tends to be leached from leaves in greater quantities than Mg (Gjengedal 1996). At FEF, after 5 years of experimental additions of ammonium sulfate at twice the ambient input levels, it was concluded that N additions to WS3 had resulted in increases in NO_3^- production and leaching and loss of Ca and Mg (Adams et al. 1993, Adams 1999).

Community Implications

The concentration of a given nutrient in foliage is clearly linked to the pool of that nutrient in soil, but this linkage is mediated by physical access to nutrients, absorption of the accessible nutrients, and allocation of the nutrient relative to C in the plant, all of which vary independently with a wide range of biotic and abiotic factors (Fyles et al. 1994). One factor contributing to nutrient availability is nitrogen saturation. As a result of increasing industrial inputs into the atmosphere and transport of pollutants over large regions, more forests are becoming N saturated and subsequently show symptoms of decline (Hallett and Hornbeck 1997).

Forest decline is brought about by changes in nutrient cycling, such as nutrient deficiencies and also by the impacts of increased ionic Al in soil, including toxicity, antagonism with nutrient uptake, and imbalances caused by increased N availability (Hallett and Hornbeck 1997). Nitrogen additions have been shown to significantly alter foliar chemistry, morphology, and physiology within montane red spruce (Schaberg et al. 1997). Some forests are even experiencing shifts in species composition as a result of N saturation. In many eastern deciduous forests, oaks and hickories are reported in decline, accompanied by increases in the abundance of more mesophytic species, such as sugar maple, tulip-poplar, and black cherry (Decker and Boerner 1997). Research at FEF indicates that both watersheds used in our study, regardless of treatment, exhibit symptoms of N saturation (Gilliam et al. 1996). Peterjohn et al. (1996) reported that WS3 at FEF already showed seven symptoms of N saturation, including high relative rates of net nitrification and long-term increases in streamwater concentrations of nitrate and base cations. However, there have been no visible symptoms of decline (Adams 1999).

Community composition may account for a significant portion of the variability in the response of forested watersheds to similar levels of elevated N deposition (Peterjohn et al. 1999). Although nitrogen enrichment may initially result in increased productivity, it may not be uniform among species and growth forms (Decker and Boerner 1997). Studies conducted by Lovett and Rueth (1999) show that beech and maple respond differently to high N deposition. In beech-maple stands, there is a highly significant interaction between N deposition and species, indicating that soils under the two species respond differently to N deposition (Lovett and Rueth 1999). Recent studies by Peterjohn et al. (1999) suggest that sugar maples may have a limited capacity to compete for available NO_3^-N, a trait that may make sugar maple more susceptible to an early onset of N saturation (Peterjohn et al. 1999). Previous work at Mt. Ascutney in Vermont associated N fertilization with reduced growth and increased mortality in red spruce (Schaberg et al. 1997).

Net mineralization and nitrification of entire forest watersheds and the response of nitrification to N deposition, may depend on species composition (Lovett and Rueth 1999). Nitrification produces nitrate, which can be lost in draining water – stream nitrate concentration is a key indicator of saturation and may depend on species composition as well as N accumulation (Lovett and Rueth 1999). It would also suggest that management practices, or natural changes, which favor certain species, might delay or accelerate the onset of N saturation and the potentially negative changes associated with this process (Peterjohn et. al. 1999). It is suggested that prior land use history (100-200 years) can play a significant role in preconditioning a forest's response to nitrogen deposition (Aber et al. 1998). The greater the previous extraction of N from agricultural conversion, fires, and harvesting, the greater the nitrogen limitation on net photosynthesis and forest growth and the larger the amount of N deposition required to move the system towards saturation (Aber et al. 1998). Processes that change the species composition, such as selective harvesting, climate changes, and plant diseases (e.g., beech bark disease) may also affect the rate of saturation (Lovett and Rueth 1999).

Each nutrient determines the possible concentration range of the other, such that their ratio stays within fixed boundaries; e.g., the maximum nitrogen concentration in the

leaves that can occur is determined by the supply of P (Mohren et al. 1986). An abundance of N in soil may lead to the reduction in root growth relative to shoot growth, which can cause reduction in P uptake relative to nitrogen uptake (Mohren et al. 1986). It is possible that nutrient concentrations in this study are linked to one another in a similar fashion. On WS3, ACRU had lower N, P, Ca, and Mg concentrations, which seem to be linked to an increase in Al concentrations. Also, all four nutrients had increased concentrations in LITU and this was linked to lower Al values. Only PRSE remained unchanged with regard to the relationship between the nutrients.

Large increases in soil Ca^{2+} and pH as a result of liming may precipitate Al^{3+} and create a more favorable Ca:Al ratio (Wilmot et al. 1996). Improved nutrient availability and uptake after treatment promotes a positive change in tree condition, which suggests the efficacy of lime and cation treatments (Wilmot et al. 1996). Trees in limed plots had higher Ca and Mg concentrations and higher Ca:Al ratios (Long et al. 1997). Low soil and foliar concentrations of Ca and Mg have been associated with declining sugar maple stands in Vermont (Wilmont et al. 1996; Long et al. 1997). At sites where N deposition is high, base cation fertilization is an important management option for sites where the main emphasis lies in stand vigor and wood production (Mohren et al. 1986). Such treatments may be able to alleviate symptoms of N saturation in many areas, including the hardwood forests of central Appalachia.

Chapter IV. Nutrient Ratios in Green Foliage

N:P Ratios and N:Ca Ratios

The ratio of nitrogen to phosphorus in 1992 was significantly higher in PRSE on WS3 (Fig. 14A,Table 3). Nitrogen to phosphorus ratios decreased significantly in ACRU and PRSE on both watersheds between 1992 and 2000 (Fig. 15, Table 4). The ratio of N:P decreased marginally from 1999 to 2000 in ACRU on WS3 and WS7 and in PRSE on WS3.

Nitrogen to calcium ratios were significantly higher on WS3 for ACRU, LITU, and PRSE in 1992 (Fig. 14B, Table 3). These differences between watersheds no longer existed in 2000. Nitrogen to calcium ratios decreased significantly on WS3 in ACRU and marginally in PRSE from 1992 to 2000 (Fig. 16, Table 4). On WS7, the N:Ca ratio increased significantly in LITU. Differences between 1999 and 2000 N:Ca ratios were not significant for any species.

While increased N additions did not promote higher N:P ratios on WS3 (except PRSE in 1992), other studies indicate that species in areas of high N deposition, such as Douglas fir and ponderosa pine in southern California, in Norway spruce in Sweden, and in Douglas fir in the Netherlands, exhibit higher N:P ratios (Fenn et al. 1998). It has also been found that high N:P ratios, as a result of N additions, are detrimental to larch growth (Pickens et al. 1995). Nutrient imbalances in trees, expressed as foliar element ratios (Ca:Al; Mg:N) have been linked to reduction in net photosynthesis, photosynthetic N use efficiency, forest growth, and tree mortality (Fenn et al. 1998).

The N:P ratio of the plant tissue can be used to assess nutritional status by indicating which nutrient is relatively short in supply and gives an indication of the reactions to be expected if fertilizers are applied (Mohren et. al. 1986). In wetland ecosystems, the vegetation N:P ratio has been found to discriminate between N and P limited sites (Koerselman and Meuleman 1996). At N:P ratio>16, the site is P limited. With a N:P ratio<14, the site is N-limited. If the ratio is between 14 and 16, N or P may be limiting or both may equally be limiting (Koerselman and Meuleman 1996). Also, Mohren et al. (1986) suggest that in a terrestrial system, a N:P ratio of 20-30 is associated with a P deficiency in Douglas fir. Although Douglas fir is needle-bearing rather than deciduous (like the species in our research), such relative values may help

to determine which nutrients are limited in N saturated systems. Based on the values from these two studies, ACRU on WS3 is becoming P-limited, whereas ACRU on WS7 is moving towards N limitation (Fig. 15). Both LITU and PRSE on WS3 and WS7 appear to be N-limited.

Ca:Al Ratios and Mg:Al Ratios

Calcium to aluminum ratios in 1992 were significantly lower on WS3 in ACRU, LITU, and PRSE (Fig. 17A, Table 3). By 2000, the only significant difference was in ACRU on WS3. From 1992 to 2000, the Ca:Al ratio increased significantly on WS3 in both ACRU and LITU and on WS7 in ACRU (Fig. 18, Table 4). The ratio of Ca:Al also increased significantly in ACRU on both WS3 and WS7 from 1999 to 2000.

The magnesium to aluminum ratio in LITU was significantly lower on WS3 in 1992 (Fig. 17B, Table 3). Between 1992 and 2000, the Mg:Al ratio increased significantly on WS3 in LITU, while decreasing significantly on WS7 (Fig. 19, Table 4). The ratio also decreased marginally in PRSE on WS3. The ratio of magnesium to aluminum increased significantly from 1999 to 2000 in ACRU.

Low Ca:Al and Mg:Al ratios are related to symptoms of forest decline (Hallett and Hornbeck 1997). Also, it has been found that Ca:Al imbalances can be induced by experimental increases in N availability and therefore it has become an unifying principle in forest decline research (Aber et al. 1998). Nitrogen deposition promotes soil acidification, which leads to low Ca:Al and Mg:Al ratios in the soil and inhibition of Ca/Mg uptake and Ca/Mg deficiencies in foliage (Hallett and Hornbeck 1997). However, each species shows different Ca:Al or Mg:Al ratio thresholds for inhibition of growth and/or nutrient uptake (Decker and Boerner 1997).

Decker and Boerner (1997) found that low Ca:Al ratios significantly affected growth rate and leaf production in LITU seedlings. Low Ca:Al ratios also tend to decrease overall production in the species (Decker and Boerner 1997) and are the result of decreased Ca concentrations in the presence of higher Al concentrations. Calcium to aluminum ratios were considerably lower in LITU on both WS3 and WS7, as compared to ACRU and PRSE. Magnesium to aluminum ratios were also lower on WS3 for LITU. These results suggest that of the three species studied, LITU may already be exhibiting potential signs of decline.

Chapter V. Nutrient Resorption

Nutrient resorption plays a critical role in the overall productivity of a forest ecosystem, with as much as 34% of nitrogen and 30% of phosphorus used annually by vegetation being provided by resorption (Ryan and Bormann 1982). The process allows N and P to be readily available during periods of rapid growth and during year-to- year fluctuations in nutrient availability (Ryan and Bormann 1982). Several variables appear to influence resorption, including soil fertility, species of tree, and foliar nutrient concentrations. Each variable is susceptible to the effects of N saturation and will respond differently to excess amounts of N. Ultimately, these variables have the potential to affect one another and lead to disruptions in normal resorption processes.

Soil fertility is the most widely studied of the proposed factors influencing nutrient resorption. Some research indicates that resorption processes are more intensive on nutrient poor sites (Stachurski and Zimka 1975; Boerner 1984); while other studies have found that trees on nutrient rich sites are more efficient at nutrient resorption (Ryan and Bormann 1982; Zhang and Allen 1996). Nitrogen resorption in oaks was reported to be 41-140% higher on less fertile sites and phosphorus resorption was 25-86% higher on less fertile sites (Boerner 1984). Research at FEF supports the findings of Stachurski and Zimka (1975) and Boerner (1984), in that N resorption values were 4.2-45% higher on WS7 (control) and P resorption was 6.5-39.5% higher on WS7 in both ACRU and PRSE.

Stachurski and Zimka (1975) found resorption values ranged from 17-36% on nutrient poor sites and from 2.4-4% on nutrient rich sites. Overall, increased N inputs did not promote such wide ranging changes in resorption efficiencies between watersheds at FEF. Nitrogen resorption efficiency values ranged from 65.5 – 71.3% on WS3 and from 74 – 81% on WS7 in 1999 (Fig. 20). In 2000, N resorption efficiencies still remained lower overall on WS3, with values ranging from 42.5 - 75.1% on WS3 and from 73.8 - 81.0% on WS7. LITU on WS3 experienced a slight 1.73% increase in N resorption efficiency over LITU on WS7 (Fig. 20). Both ACRU and PRSE exhibited significant differences in N resorption values between watersheds, with ACRU being 82.4% lower on WS3 ($p=0.078$) and PRSE being 18.8% lower on WS3 ($p=0.038$) (Fig. 20).

Phosphorus resorption efficiency values were also higher on WS7 in 1999 with values ranging from 69.5 – 82.4%. However, P resorption was 2.51% higher on WS3 for LITU. While differences existed between watersheds, none were found to be significant (Fig. 21). In 2000, the same trend for P resorption was carried over from 1999 on WS3, with efficiency values ranging from 54.0 - 79.1%. Values for LITU on WS3 remained slightly higher than WS7 by 3.07% (Fig. 21). Comparisons between 1999 and 2000 data show that a significant difference exists only between P resorption efficiencies in ACRU on WS7, with 2000 values being 11.9% higher than 1999 ($p=0.083$). Although not significant, other differences exist as well. Between 1999 and 2000 on WS3, N resorption efficiencies decreased in ACRU and PRSE and increased in LITU. Differences in P resorption efficiency values range from a decrease of 35.9% in ACRU to an increase of 9.86% in LITU on WS3, and increases on WS7 ranging from 4.52 - 11.9%.

Although these data support previous studies suggesting that species on "nutrient poor" sites have a higher resorption efficiency, it is evident that differences in resorption processes may not be simply a matter of "nutrient poor" versus "nutrient rich" sites. Higher resorption efficiency values for species on WS7 may indicate that species on WS3 are experiencing disruptions in physiological processes, such as resorption, as a result of the elevated N inputs. Yearly variations in other factors, such as nutrient concentrations, rainfall, and temperature, could also potentially alter the resorption efficiencies, accounting for the differences between 1999 and 2000 data.

Variability among tree species is also evident in this study, with LITU resorption values illustrating such differences. Killingbeck and Costigan (1988) suggest that soil fertility may only act as a strong selection pressure – one that affects the conservation of plant elements in general and that specific adaptation evolved by plants to conserve elements may vary among species and sites. Additional research proves that resorption is highly variable among tree species (del Arco et al. 1991), with interspecific differences being evident in the proportion of N (0-79%) and P (0-89%) removed from leaves of deciduous species prior to senescence (Chapin and Kedrowski 1983). Tulip-poplar had lower N resorption values on WS7 in 2000 and lower P resorption values on WS7 in both 1999 and 2000, whereas ACRU and PRSE had higher resorption values

on WS7. Tulip-poplar, as mentioned in Chapter III, shows increased sensitivity to Al as a result of N treatments and also experiences subsequent decreases in foliar Ca and Mg concentrations. Such variations in the availability of essential nutrients and the response of the species to such flucuations could account for the difference in resorption efficiences.

In addition to soil fertility and species, nutrient concentrations in presenescent leaves have been shown to have a large influence over resorption processes (Chapin and Kedrowski 1983; Killingbeck and Costigan 1988). The linkage between resorption and foliar element concentration may lie in the relationship between foliar element concentrations and nutrient use efficiencies (Killingbeck and Costigan 1988). Nutrient use efficiencies decrease as element concentrations increase, therefore, natural selection should then act to increase resorption efficiency when nutrient use efficiency is low (foliar nutrient concentrations high) (Killingbeck and Costigan 1988). This was found to be the case on with our study – species that exhibited higher foliar N and P concentrations also exhibited lower N and P resorption efficiencies (WS3), whereas species with lower foliar N and P concentrations exhibited higher N and P resorption efficiencies (WS7).

It is also suggested that N resorption may even rely on the presence of another element, such as K or P (Ostman and Weaver 1982). Our results seem to indicate that there is a link between the concentration of N and P within a species, therefore it is possible that P is a determining factor in the amount of N a tree is capable of resorbing. Other nutrients such as Ca or Mg, or even Al with its detrimental effects, may also have the potential to regulate the resorption process.

Timing of abscission was not considered in this study; however, it is another factor that needs to be researched further. Abscission timing has been shown to have a strong influence on resorption efficiency in *Populus tremuloides* (Killingbeck et al. 1990) and variations in the timing of abscission may affect resorption efficiency in other species as well (del Arco et al. 1991). Gradual leaf loss may be an adaptation to nutrient and water stress (del Arco et al. 1991), both of which can be induced as a result of N saturation. Monitoring changes in the timing of abscission may then be used to indicate disruptions in nutrient dynamics due to N saturation.

Chapter VI. Conclusions

Our preliminary data suggest that plant nutrient responses to N saturation shown in earlier studies may be transient and non-linear, emphasizing the complexity of the mechanisms that lead to an alteration of plant nutrient interactions. Although ecosystem-level effects are becoming better understood through numerous studies, clearly more work is needed to make the vital link between plant ecophysiological responses to excess N and the responses of ecosystem processes.

The effects of atmospheric deposition are not uniform among tree species. However, it may be possible, through monitoring trends in foliar nutrient dynamics, nutrient concentrations, and nutrient ratios, to develop a range of values that are indicative of the early stages of decline. With such data, it would be possible to research treatments that could alleviate symptoms of decline and potentially halt the decline process in forested systems.

Our research supports and strengthens the findings of previous studies, however, our data only looks at values from two consecutive years and it is evident that more research is needed. Differences in resorption have been found to depend not only on soil fertility, but also on tree species and nutrient concentrations. There is also the possibility that the results may only be short-term due to deposition of N. Longer-term studies are needed to determine what other processes may affect resorption and to what extent these factors influence one another.

The potential for forest decline in N saturated systems intensifies the need for further research. As the population of planet Earth increases, so do the demands on industry. By gaining an understanding of how pollution affects various ecosystems, this knowledge may bring about stricter pollution regulations and enforcement. Also, it will hopefully lead industries to search for cleaner, greener methods of producing for the masses.

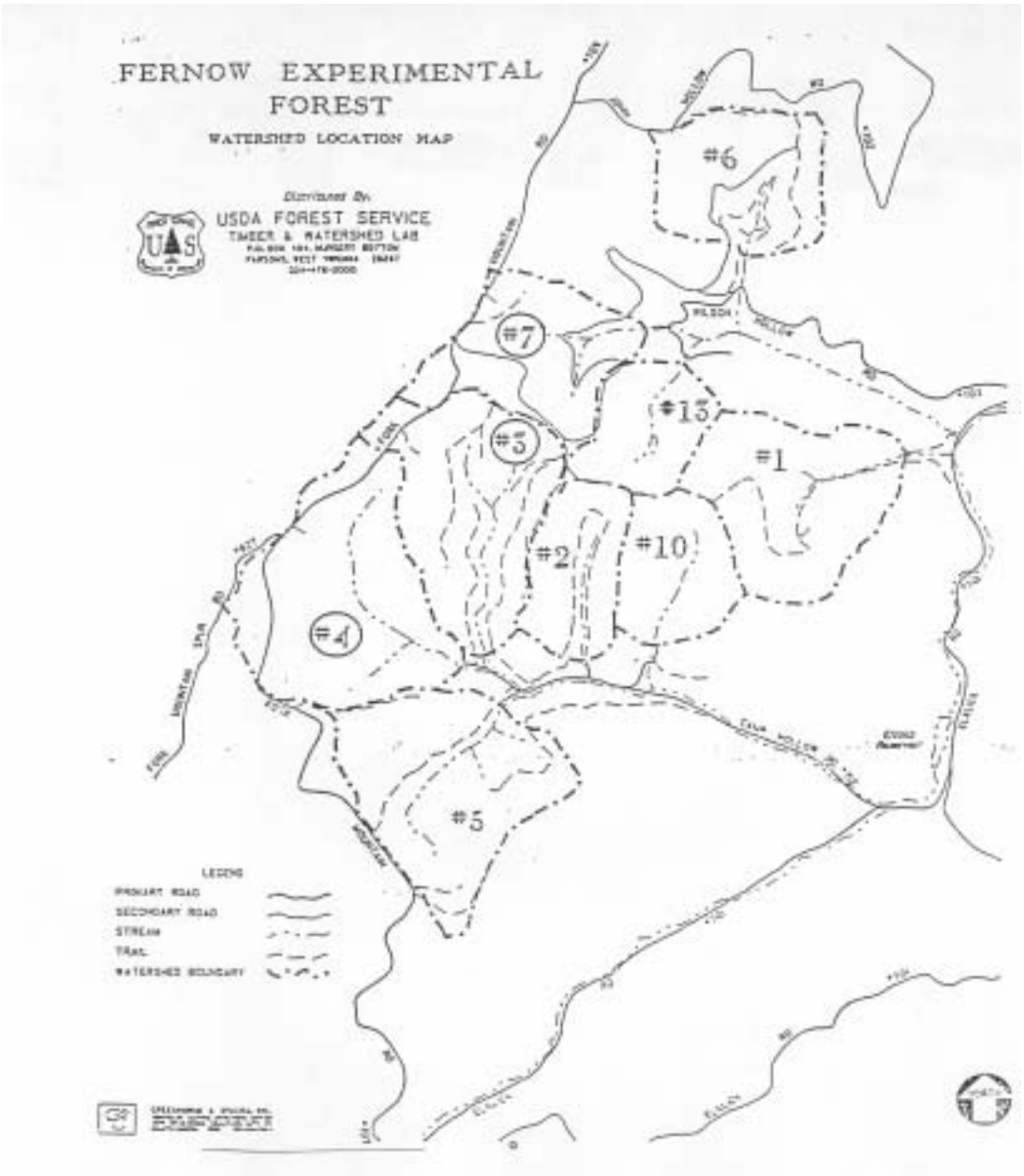

FIGURE 1. WATERSHED LOCATION MAP OF THE USDA FOREST SERVICE FERNOW EXPERIMENTAL FOREST, PARSONS, WEST VIRGINIA (TUCKER CO.). NOTE THE LOCATION OF THE TWO WATERSHEDS SAMPLED IN THIS STUDY - WATERSHED 3 (EXPERIMENTAL) AND WATERSHED 7 (CONTROL).

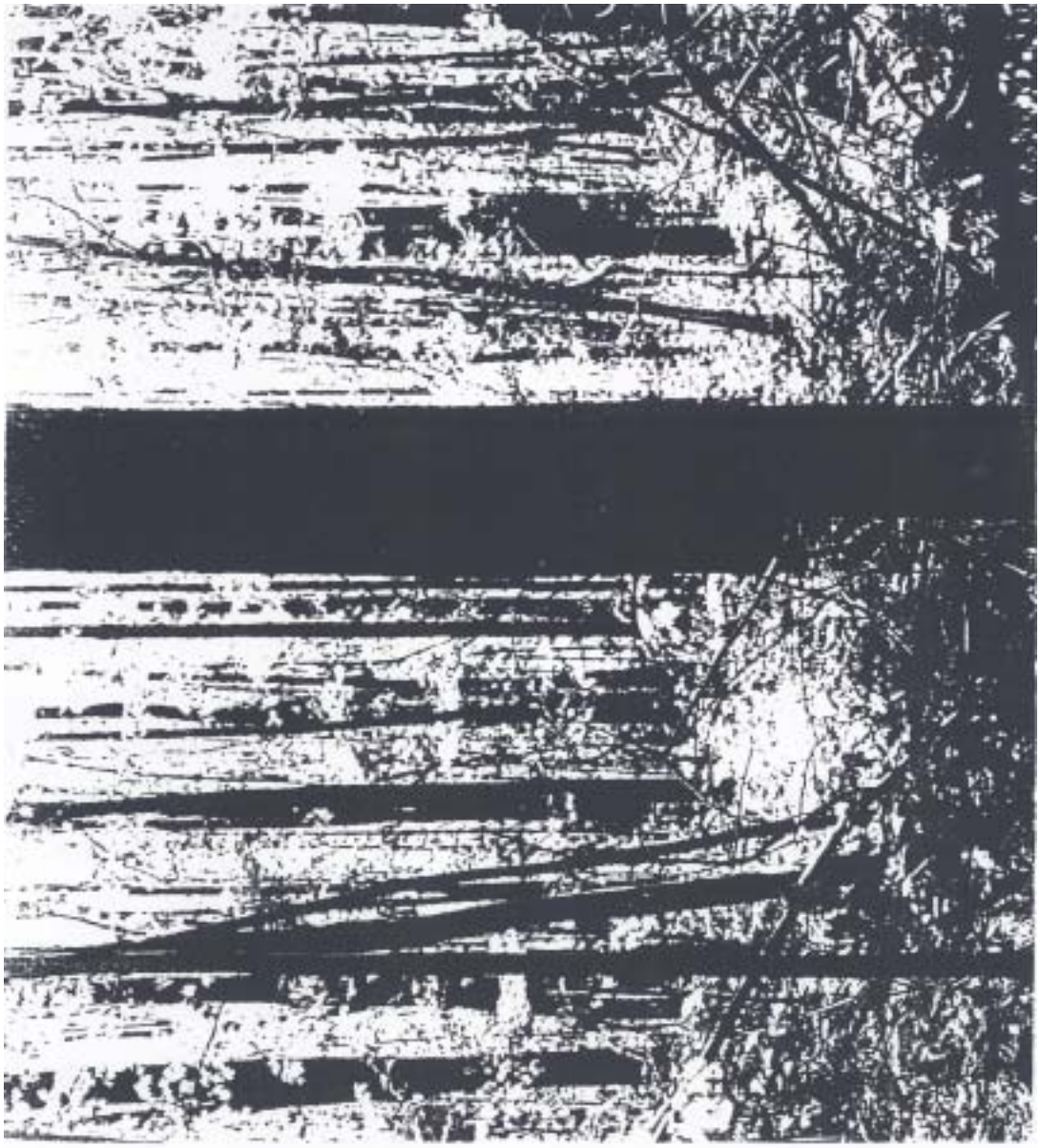

FIGURE 2. PHOTOGRAPH OF WATERSHED 3 (EXPERIMENTAL) AT THE USDA FOREST SERVICE FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

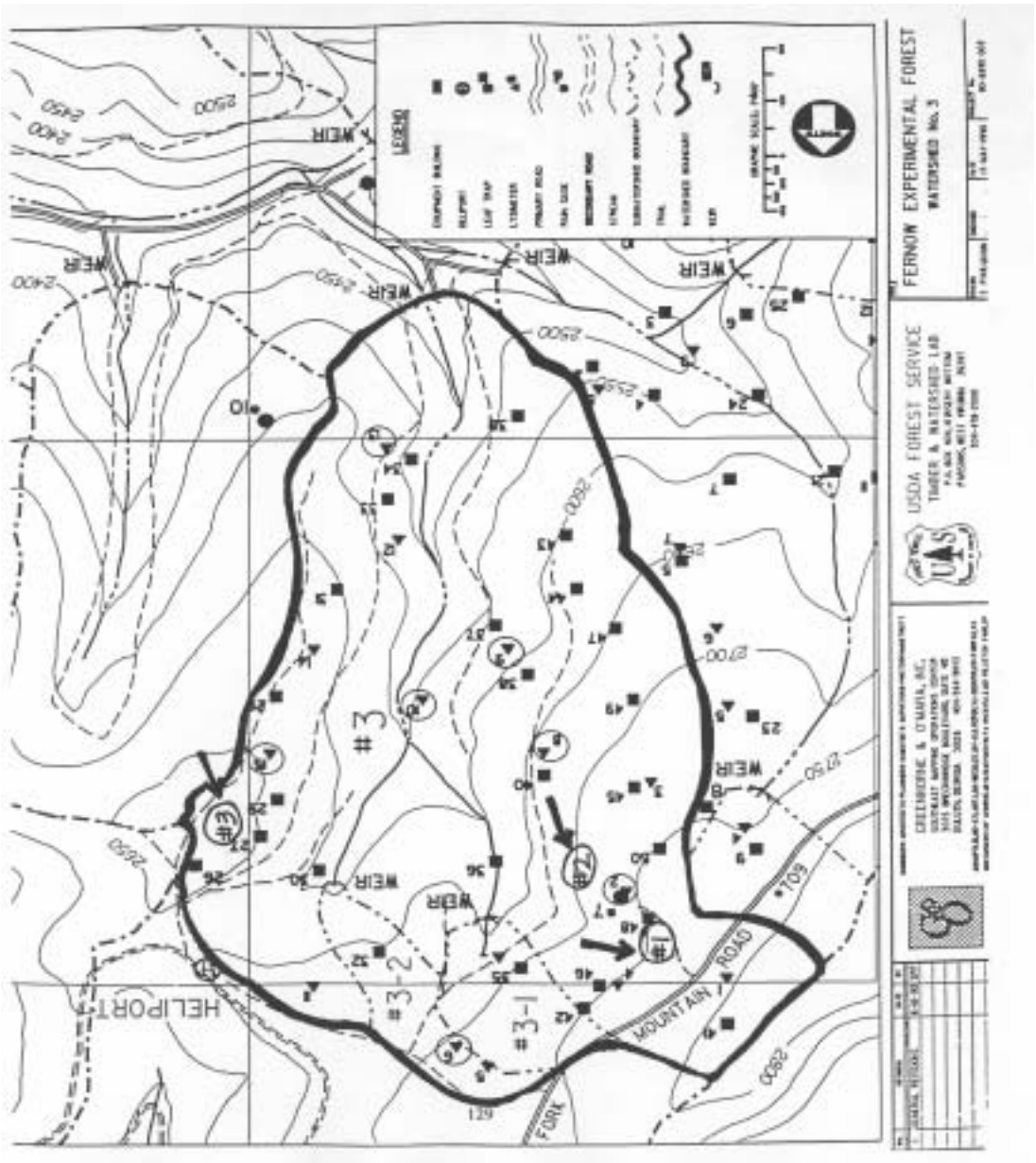

FIGURE 3. LOCATION OF SAMPLE PLOTS ON WATERSHED 3 (EXPERIMENTAL) AT THE USDA FOREST SERVICE FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

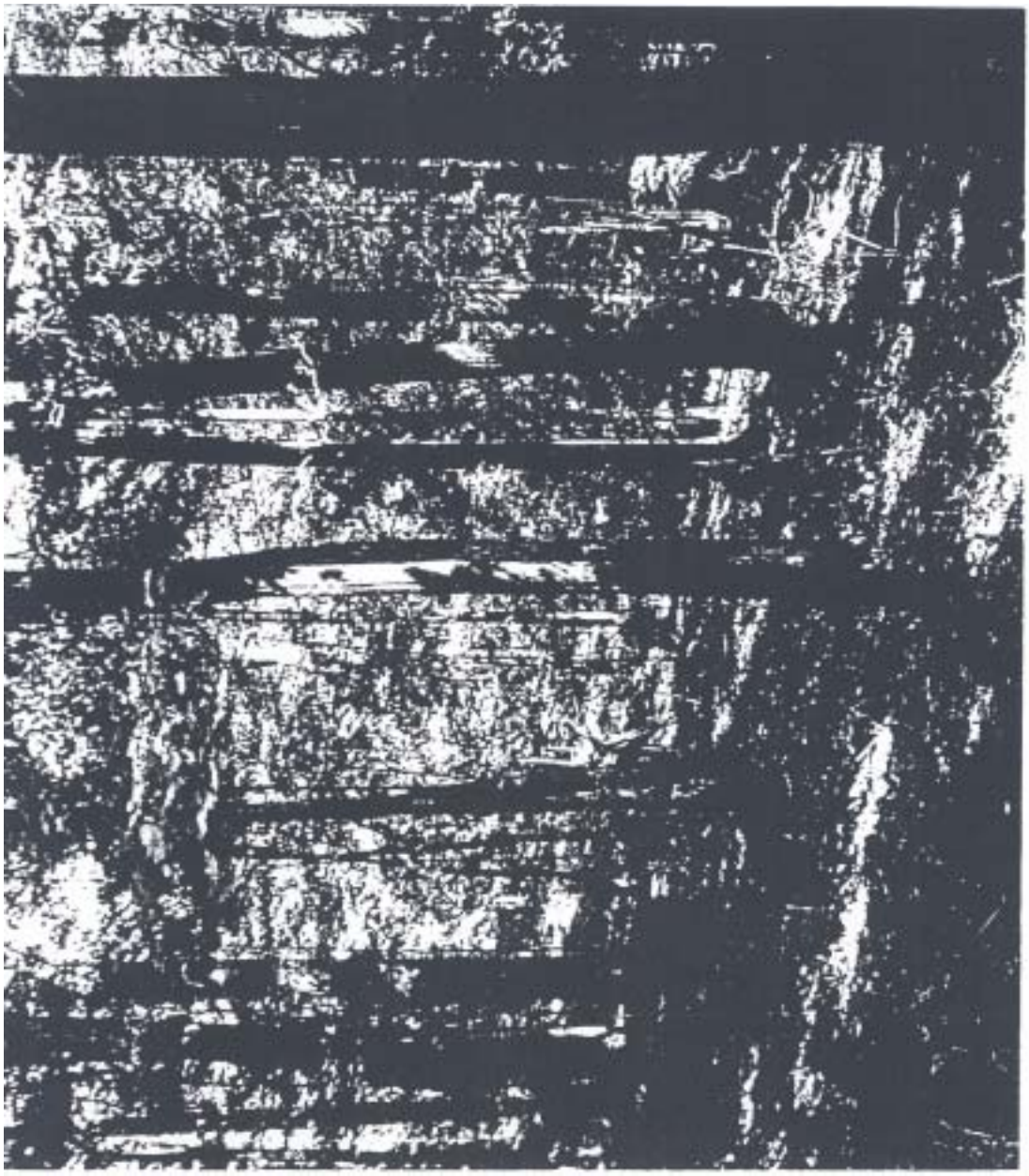

FIGURE 4. PHOTOGRAPH OF WATERSHED 7 (CONTROL) AT THE USDA FOREST SERVICE FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

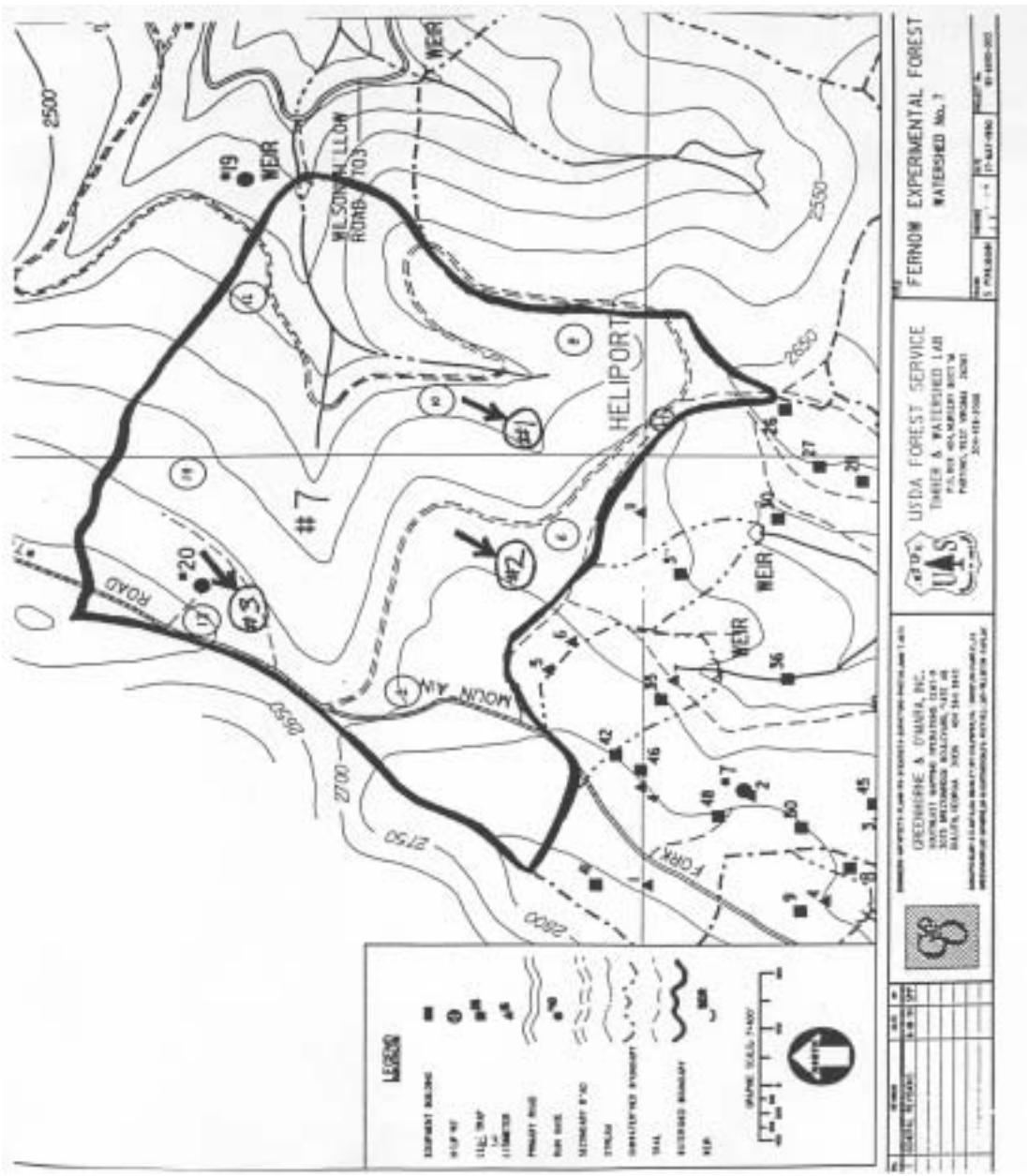

FIGURE 5. LOCATION OF SAMPLE PLOTS ON WATERSHED 7 (CONTROL) THE USDA FOREST SERVICE FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

Table 1. Significance values and percent difference values for nutrient concentration comparisons between WS3 and WS7 in 1992 and 2000 ($p<0.100$). Percent difference values are listed in parentheses.

Comparison	Year	Species	N	P	Al	Ca	Mg
WS3 to WS7	1992	ACRU	3.62E-7	6.12E-7	0.0604	3.17E-7	0.0522
			(10.4)	(10.5)	(-18.6)	(-34.5)	(-12.7)
		LITU	0.165	3.55E-6	0.0072	1.76E-4	5.81E-5
			(8.42)	(12.3)	(18.5)	(-63.7)	(-34.5)
		PRSE	2.60E-4	0.0184	0.4491	0.0041	0.0725
			(10.3)	(5.30)	(7.56)	(-35.5)	(-9.66)
WS3 to WS7	2000	ACRU	0.095	0.160	0.120	0.5979	0.7607
			(-14.97)	(-7.32)	(23.4)	(-10.5)	(-12.7)
		LITU	0.165	0.107	0.5407	0.4356	0.3312
			(87.6)	(11.3)	(-9.3)	(35.9)	(40.7)
		PRSE	0.942	0.559	0.0591	0.4356	0.3312
			(1.39)	(5.99)	(27.7)	(-38.3)	(-16.6)

Table 2. Significance values and percent difference values for nutrient concentration comparisons for WS3 and WS7 between years (p<0.100). Percent difference values are listed in parentheses.

Comparison	Watershed	Species	N	P	Al	Ca	Mg
1992 to 2000	WS3	ACRU	1.28E-8	5.7E-4	0.0669	0.0894	0.0054
			(-36.3)	(-11.9)	(-26.6)	(23.0)	(-63.3)
		LITU	0.7667	0.3586	0.2142	0.0219	0.1592
			(3.96)	(3.21)	(-22.8)	(40.9)	(21.2)
		PRSE	0.3971	0.0012	0.2136	0.0704	0.4562
			(4.18)	(14.1)	(20.8)	(29.2)	(6.93)
1992 to 2000	WS7	ACRU	0.0833	0.1167	0.0201	0.2368	0.0044
			(-7.81)	(6.74)	(-96.1)	(6.41)	(-63.2)
		LITU	0.9683	0.4246	0.4577	0.1522	0.0025
			(-0.365)	(4.29)	(8.38)	(-51.0)	(-78.5)
		PRSE	0.2768	0.0014	0.9458	0.1941	0.9765
			(6.18)	(13.5)	(-1.24)	(30.6)	(-0.416)
1999 to 2000	WS3	ACRU	0.3916	0.3007	0.2274	0.4384	0.8589
			(-5.99)	(5.69)	(-101)	(17.5)	(6.67)
		LITU	0.0363	0.0188	0.1021	0.7338	0.8768
			(18.9)	(14.3)	(37.1)	(14.9)	(5.56)
		PRSE	0.0288	0.0043	0.1805	0.9508	0.9770
			(17.2)	(23.5)	(19.4)	(2.16)	(-1.09)
1999 to 2000	WS7	ACRU	0.9599	0.1333	0.1376	0.1372	0.3268
			(0.313)	(8.11)	(-45.9)	(18.4)	(23.6)
		LITU	0.2717	0.1165	0.1346	0.8631	0.8555
			(9.64)	(12.3)	(28.5)	(-9.55)	(-12.9)
		PRSE	0.1232	0.0729	0.2666	0.2994	0.6806
			(9.66)	(14.8)	(27.7)	(40.2)	(17.1)

Table 3. Significance values and percent difference values for nutrient ratio comparisons between WS3 and WS7 in 1992 and 2000 ($p<0.100$). Percent difference values are listed in parentheses.

Comparison	Year	Species	N:P	N:Ca	Ca:Al	Mg:Al
WS3 to WS7	1992	ACRU	0.7817	3.86E-7	0.08178	0.7338
			(-0.655)	(36.1)	(-24.1)	(-4.70)
		LITU	0.4880	3.18E-5	1.38E-5	4.79E-5
			(-4.26)	(42.1)	(-102.6)	(-62.7)
		PRSE	0.0299	3.33E-4	0.0016	0.1702
			(5.54)	(33.8)	(-47.6)	(-16.4)
WS3 to WS7	2000	ACRU	0.155	0.9508	0.0343	0.2839
			(7.24)	(-1.54)	(-47.7)	(-43.4)
		LITU	0.802	0.5458	0.4044	0.3225
			(1.16)	(-34.7)	(47.7)	(50.9)
		PRSE	0.802	0.4757	0.2216	0.2887
			(5.70)	(21.6)	(-90.3)	(-66.3)

Table 4. Significance values and percent difference values for nutrient ratio comparisons between years (p<0.100). Percent difference values are listed in parentheses.

Comparison	Year/Watershed	Species	N:P	N:Ca	Ca:Al	Mg:Al
1992 to 2000	WS3	ACRU	2.1E-8	0.0066	0.0125	0.2554
			(-24.1)	(-81.8)	(36.5)	(-32.9)
		LITU	0.9940	0.1599	0.0051	0.0467
			(0.108)	(-41.9)	(56.3)	(38.7)
		PRSE	0.0019	0.0872	0.8924	0.0819
			(-21.6)	(-49.9)	(6.71)	(-50.6)
1992 to 2000	WS7	ACRU	0.0281	0.1233	0.0020	0.9173
			(-16.5)	(-15.0)	(46.7)	(2.98)
		LITU	0.5417	0.0376	0.1280	0.0159
			(-5.40)	(39.0)	(-69.2)	(-103)
		PRSE	0.0926	0.3424	0.1644	0.8301
			(-8.69)	(-26.5)	(27.6)	(-5.38)
1999 to 2000	WS3	ACRU	0.0861	0.3005	0.0482	0.3723
			(-12.9)	(-29.2)	(50.8)	(42.9)
		LITU	0.2904	0.7060	0.6541	0.5078
			(5.22)	(15.5)	(-36.7)	(-50.2)
		PRSE	0.0442	0.7174	0.5799	0.5345
			(-8.14)	(10.9)	(-22.1)	(-28.5)
1999 to 2000	WS7	ACRU	0.0983	0.2877	0.06012	0.0106
			(-8.82)	(-23.8)	(40.5)	(45.6)
		LITU	0.2954	0.6989	0.4059	0.4759
			(-3.38)	(16.6)	(-72.9)	(-60.6)
		PRSE	0.2089	0.3213	0.7872	0.5422
			(-6.55)	(-38.1)	(-22.2)	(-68.6)

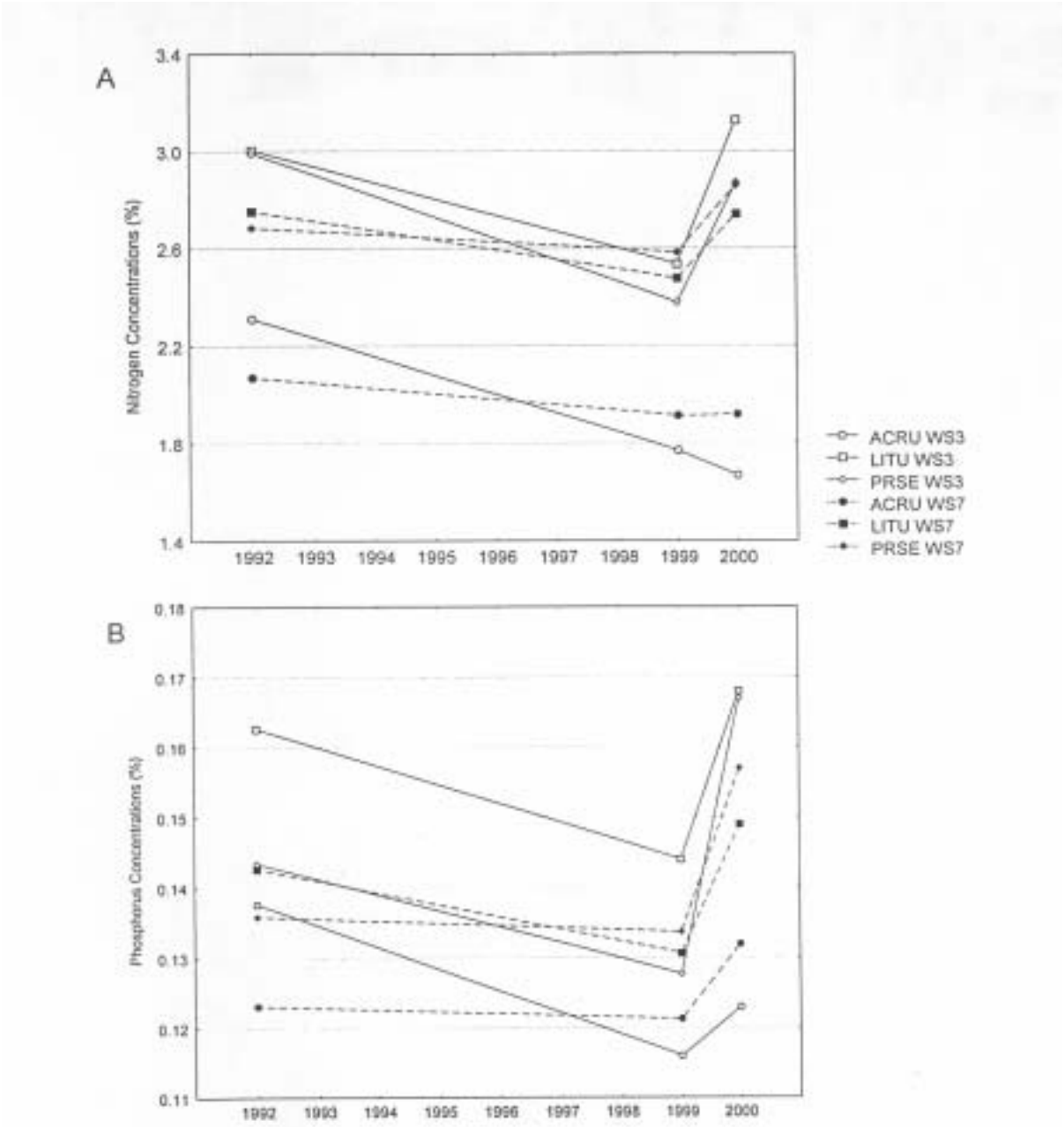

FIGURE 6A. AND 6B. TREND IN FOLIAR NITROGEN CONCENTRATIONS (6A) AND FOLIAR PHOSPHORUS CONCENTRATIONS (6B) FROM 1992 TO 2000 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) ON WS3 AND WS7 AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

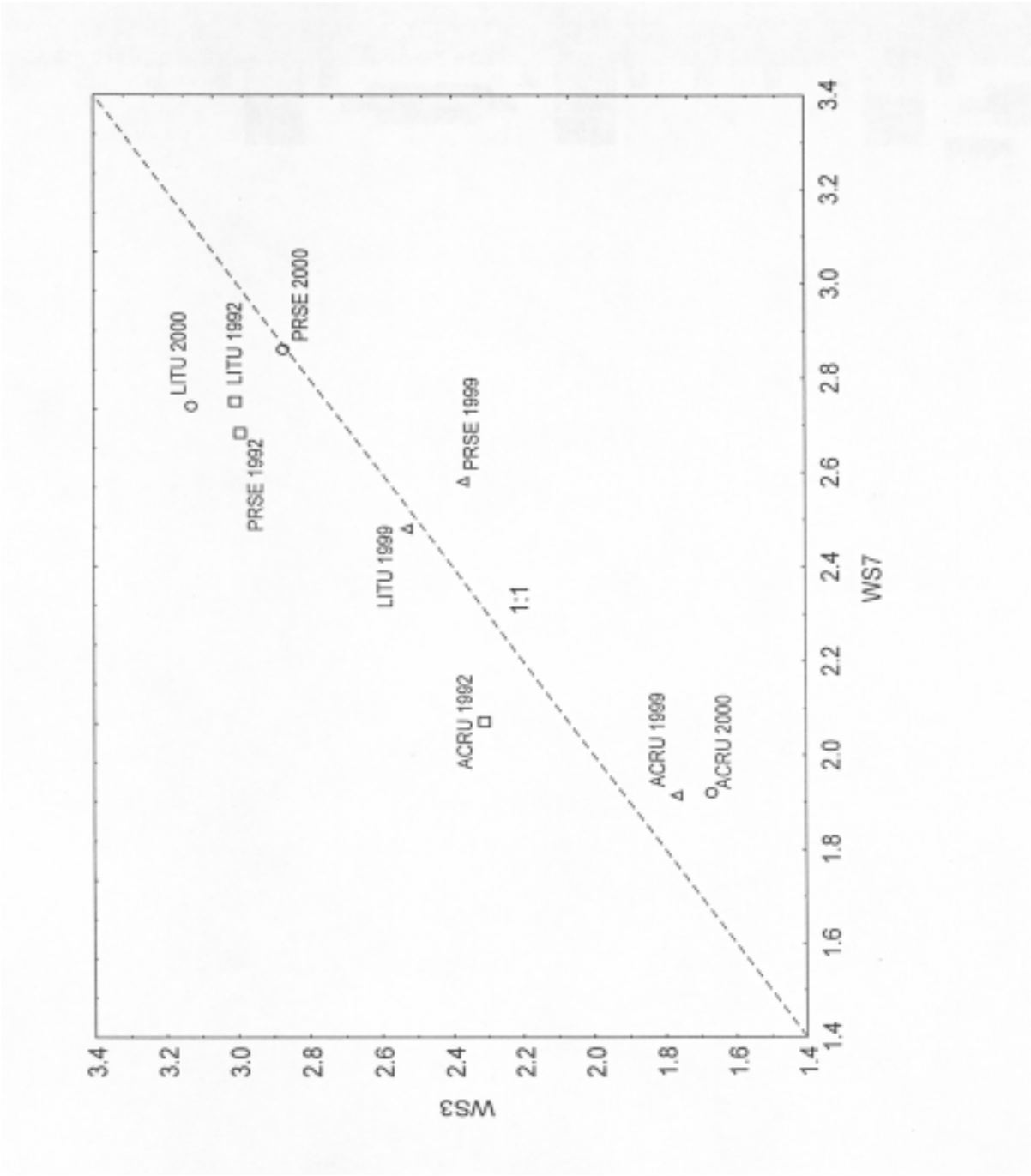

FIGURE 7. FOLIAR NITROGEN CONCENTRATION – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

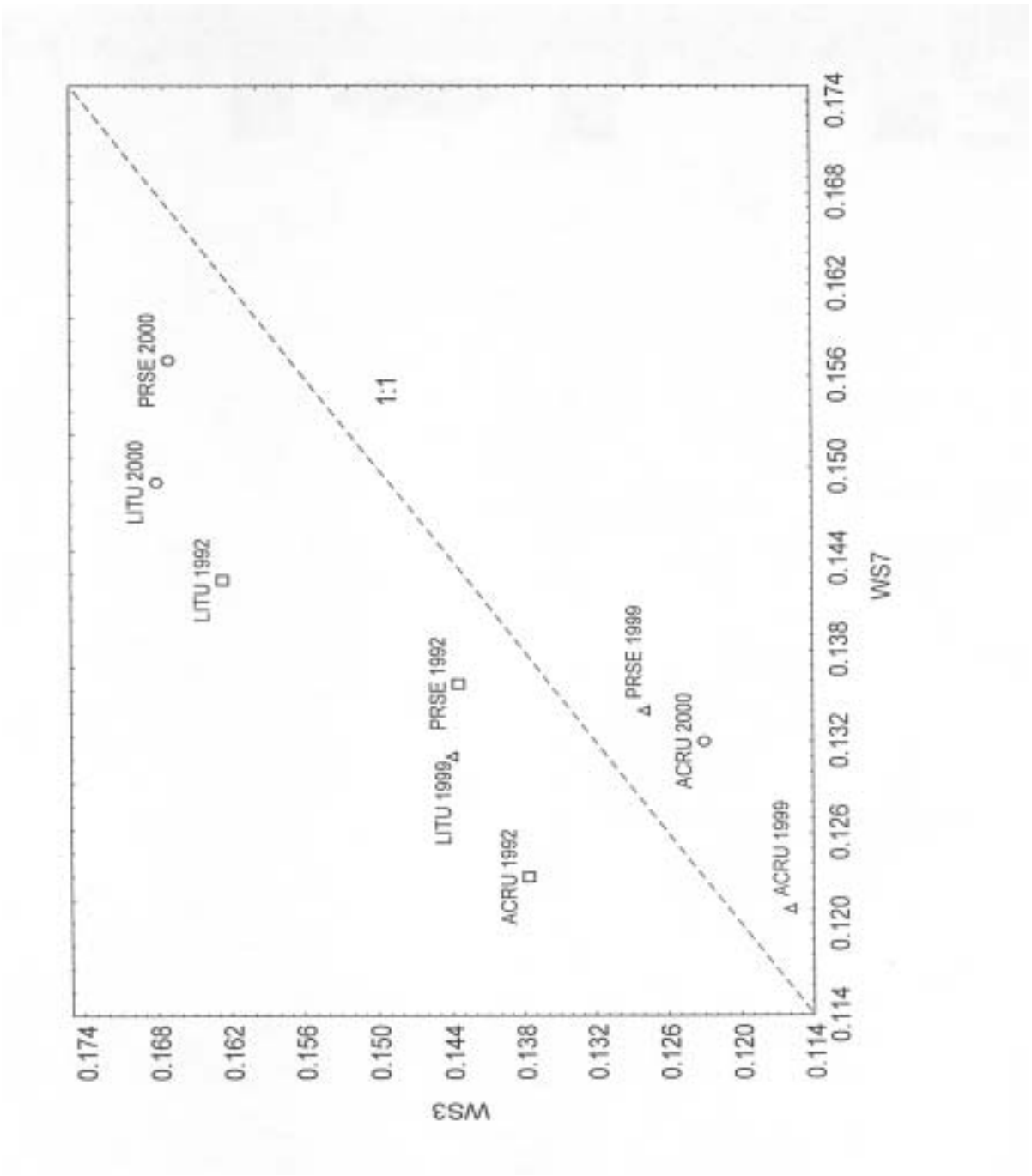

FIGURE 8. FOLIAR PHOSPHORUS CONCENTRATION – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

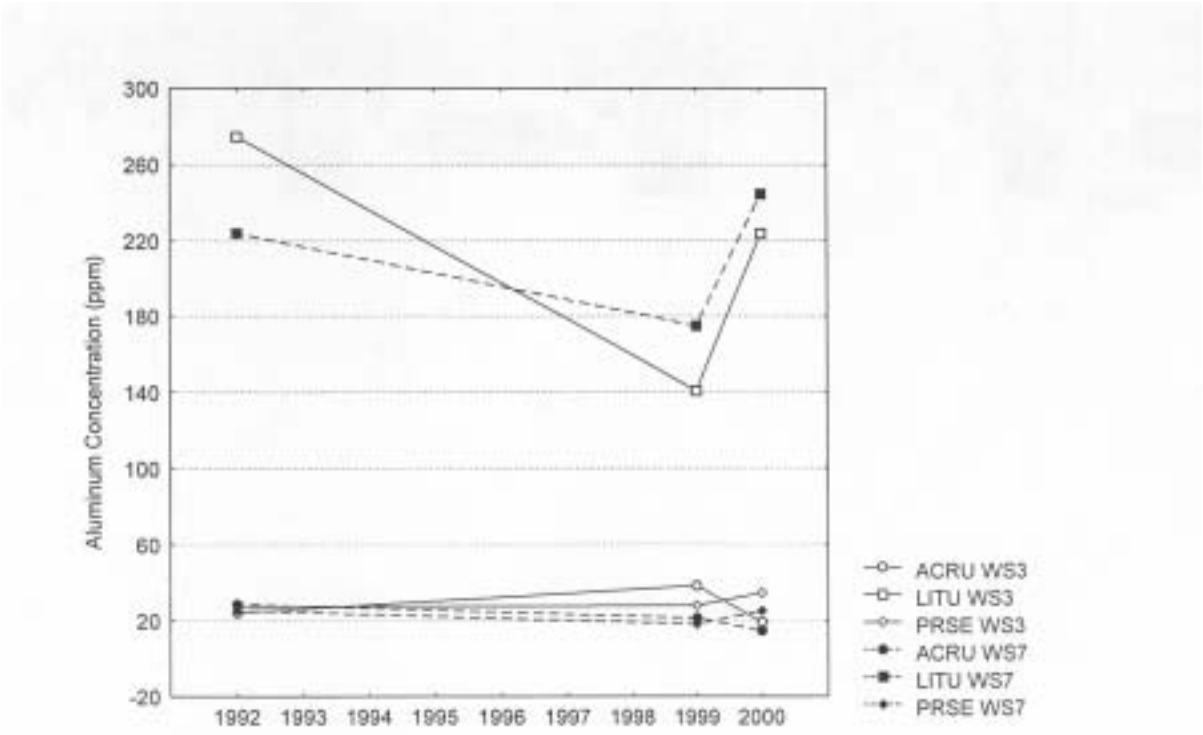

FIGURE 9. TREND IN FOLIAR ALUMINUM CONCENTRATIONS FROM 1992 TO 2000 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) ON WS3 AND WS7 AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

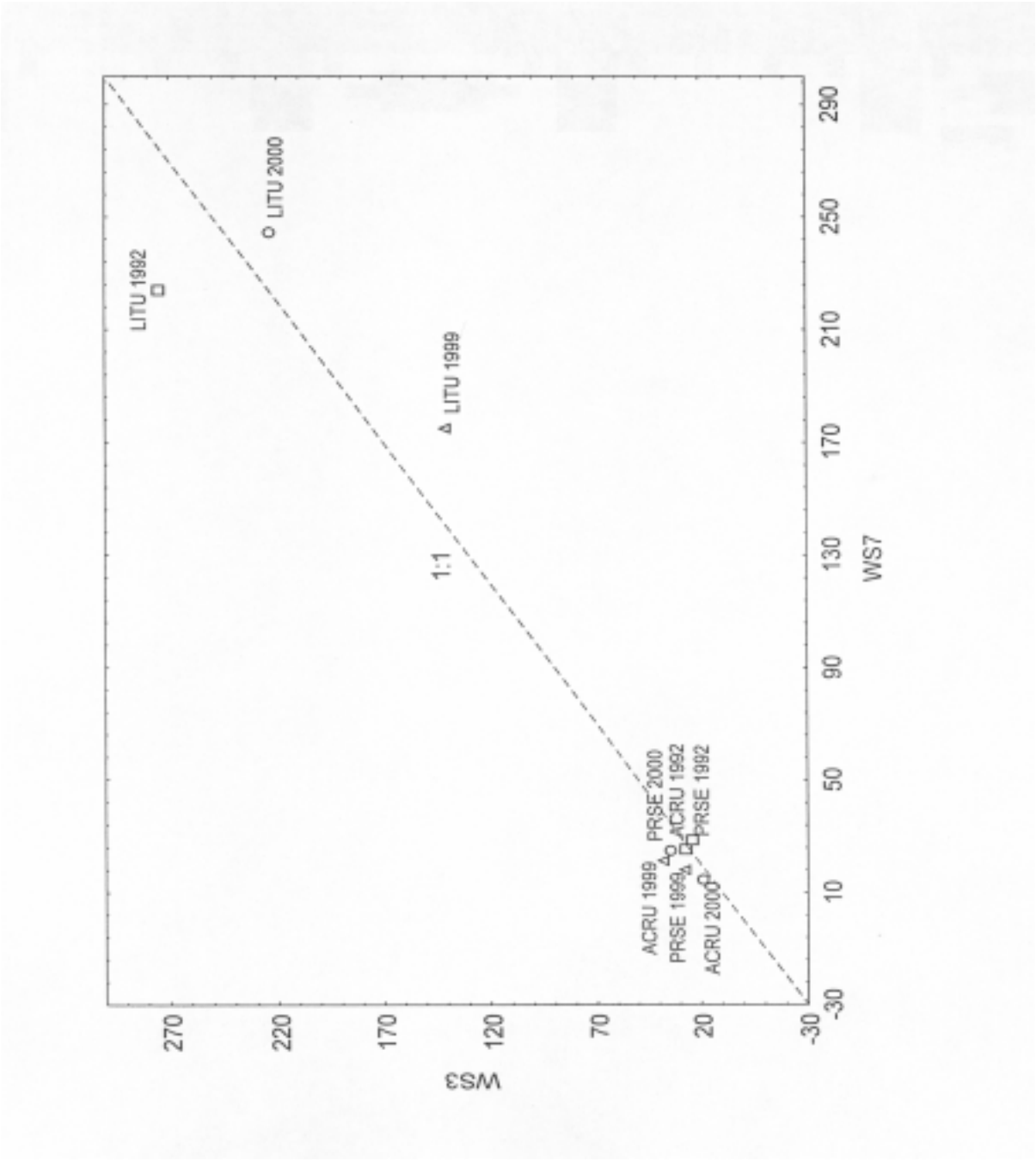

FIGURE 10. FOLIAR ALUMINUM CONCENTRATION – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

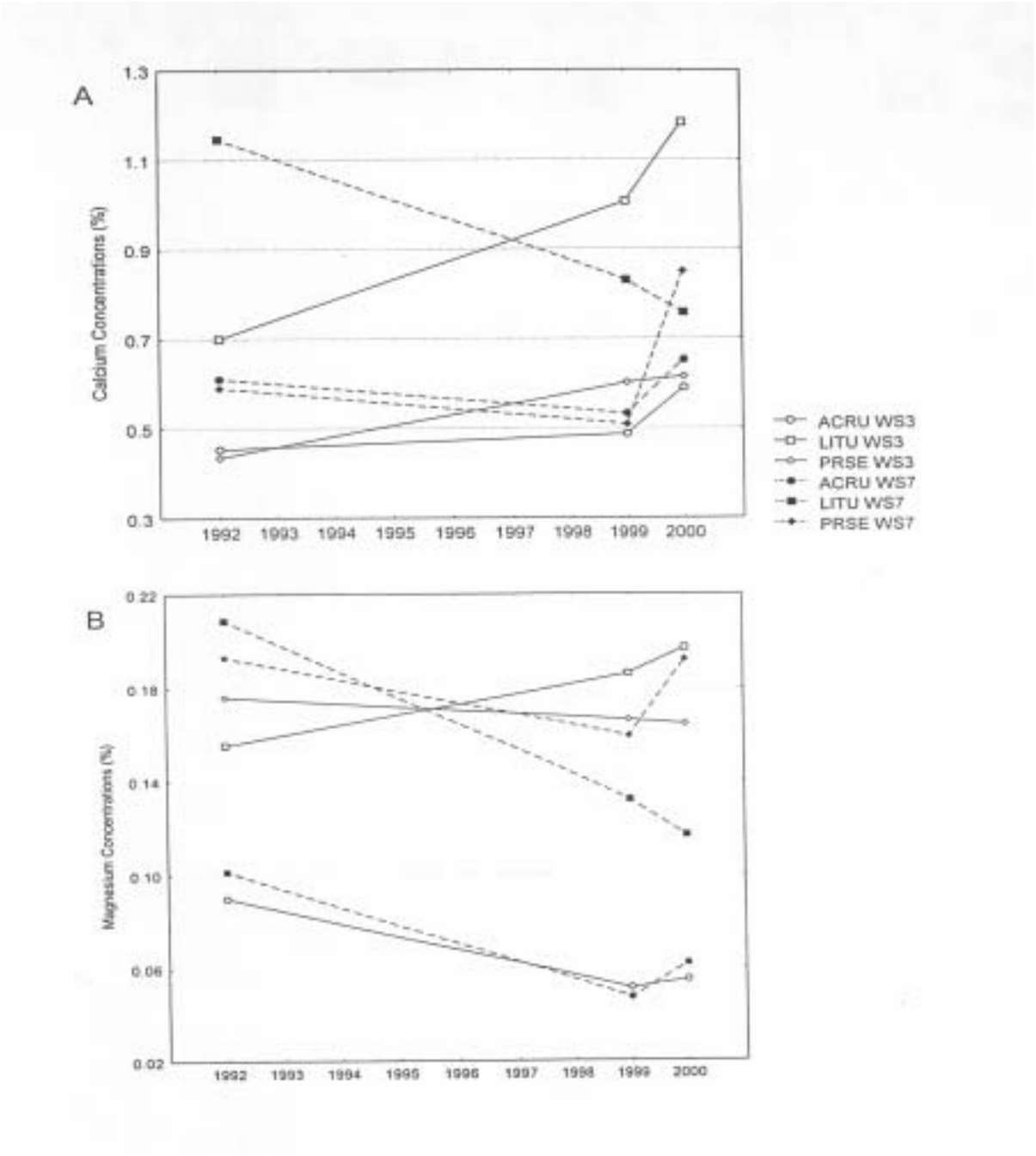

FIGURE 11A. AND 11B. TREND IN FOLIAR CALCIUM CONCENTRATIONS (7A) AND FOLIAR MAGNESIUM CONCENTRATIONS (7B) FROM 1992 TO 2000 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) ON WS3 AND WS7 AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

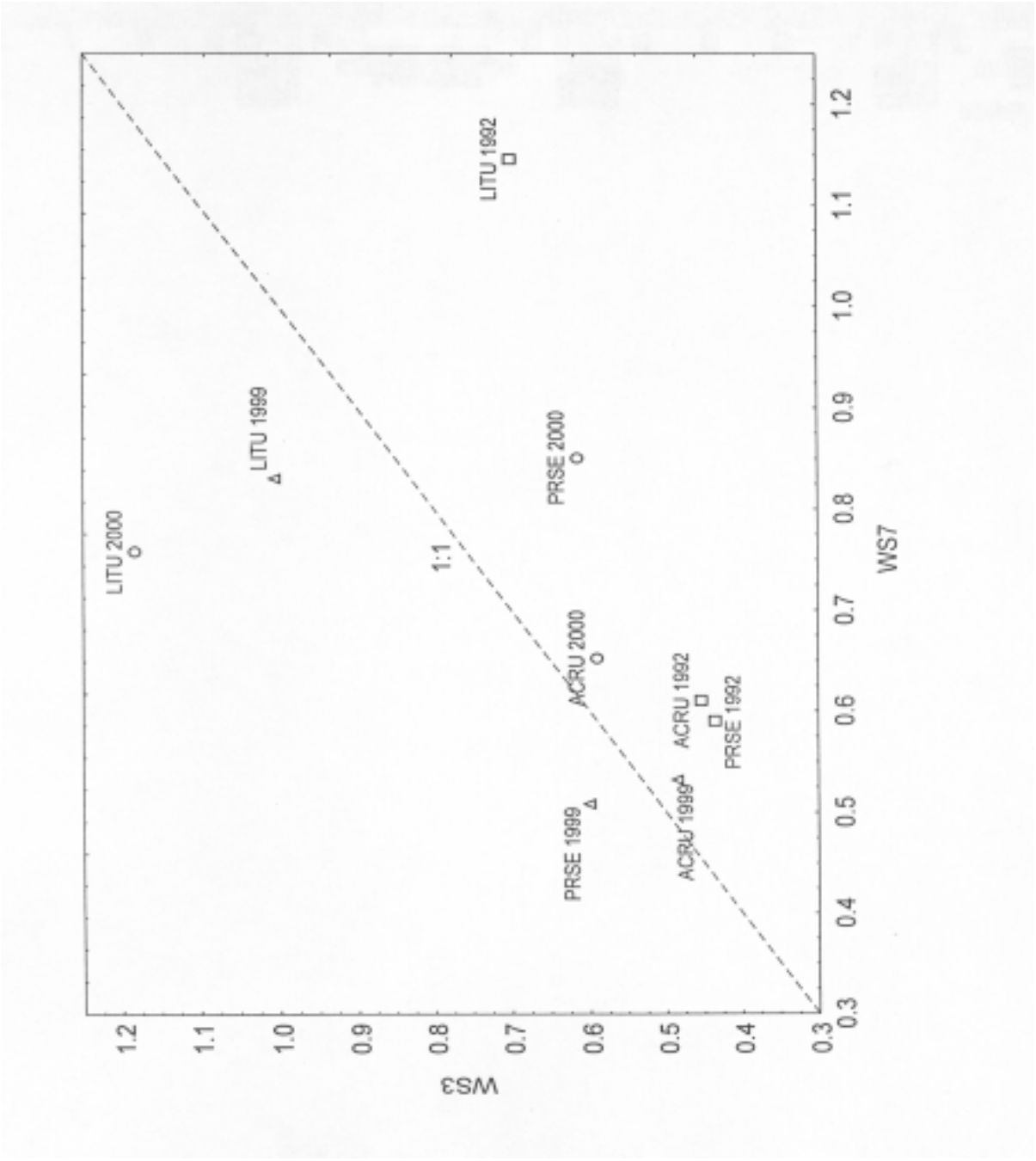

FIGURE 12. FOLIAR CALCIUM CONCENTRATION – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

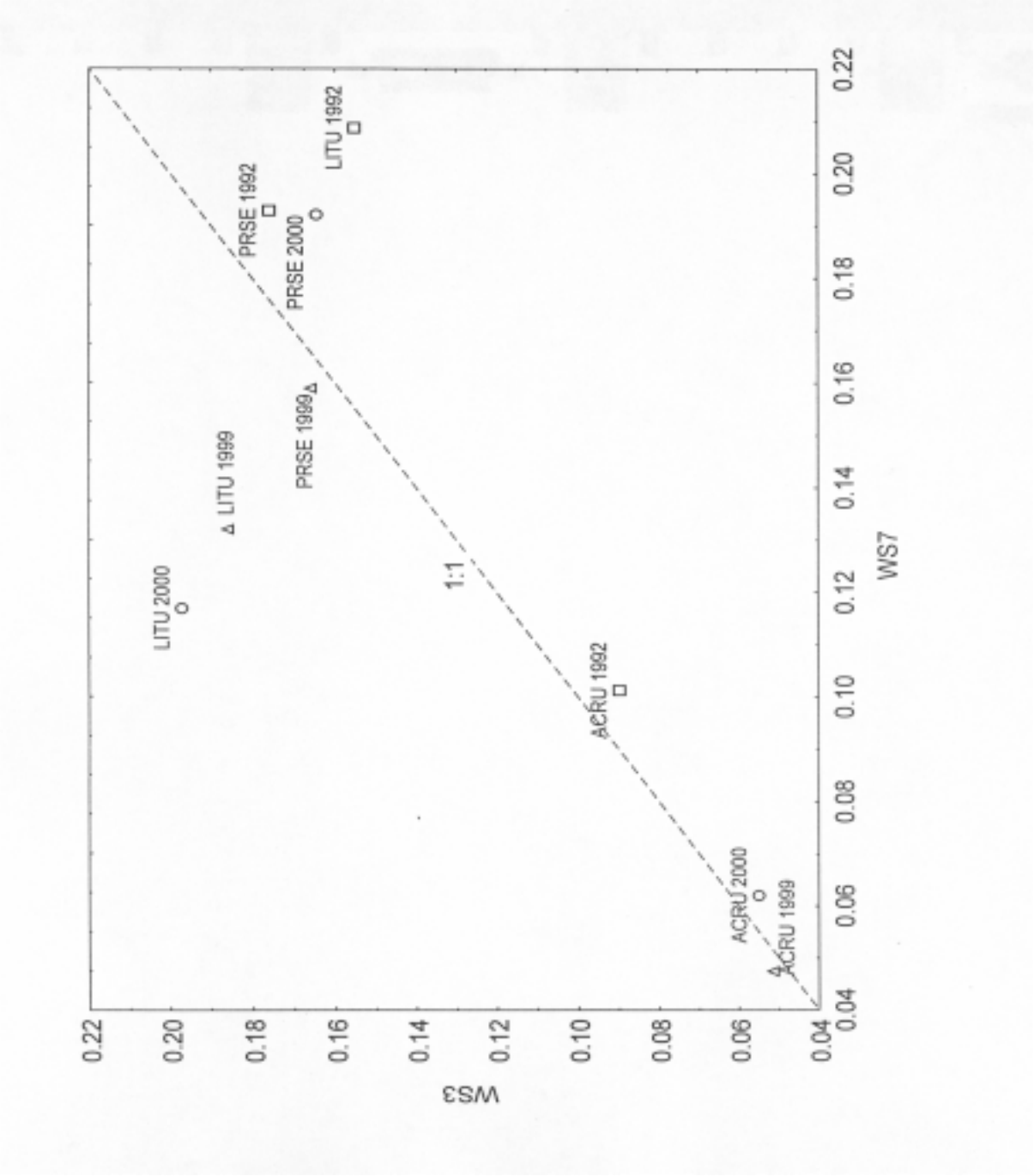

FIGURE 13. FOLIAR MAGNESIUM CONCENTRATION – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

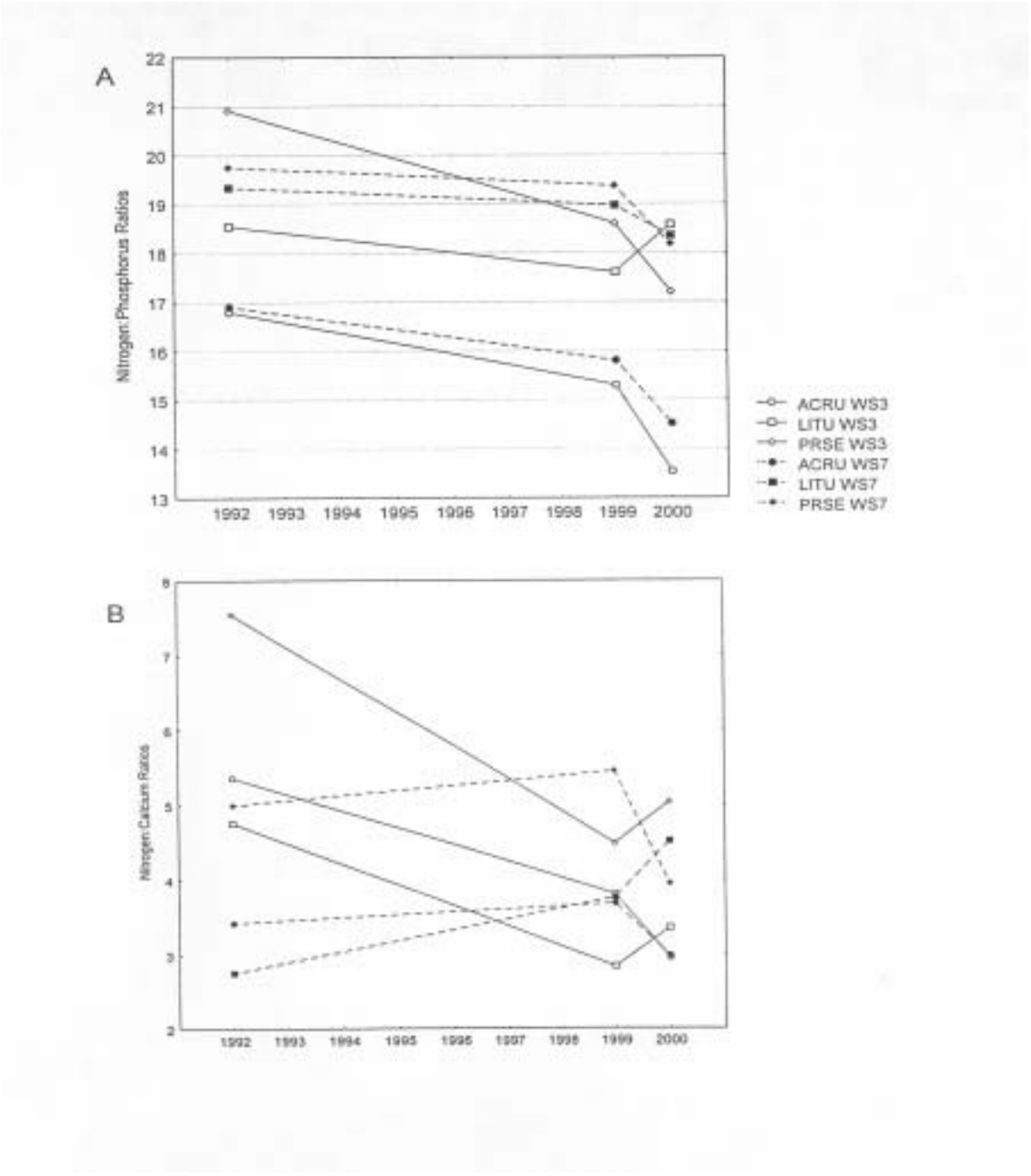

FIGURE 14A. AND 14B. TREND IN FOLIAR N:P RATIOS (14A) AND FOLIAR N:CA RATIOS (14B) FROM 1992 TO 2000 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) ON WS3 AND WS7 AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

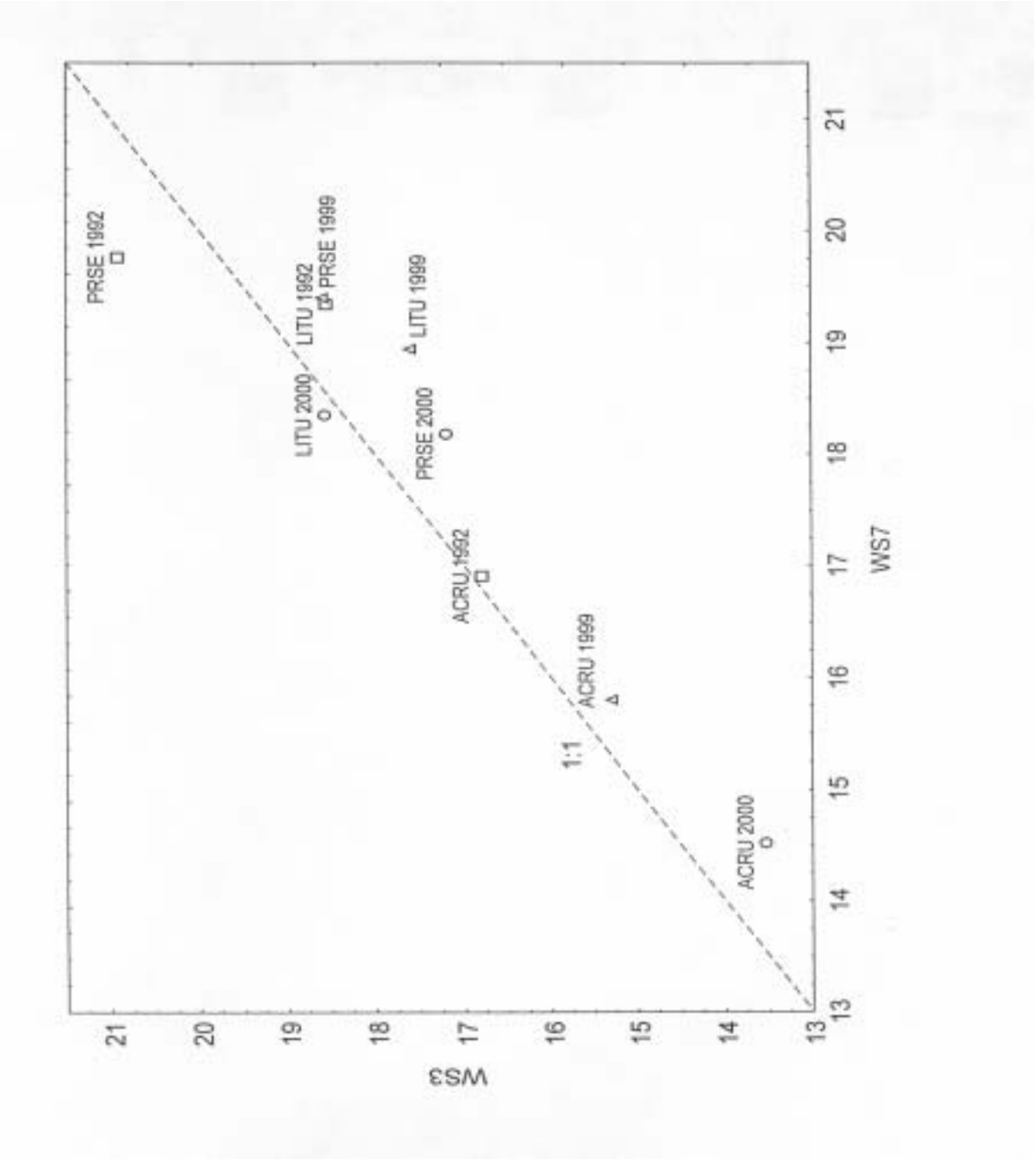

FIGURE 15. FOLIAR N:P RATIO – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

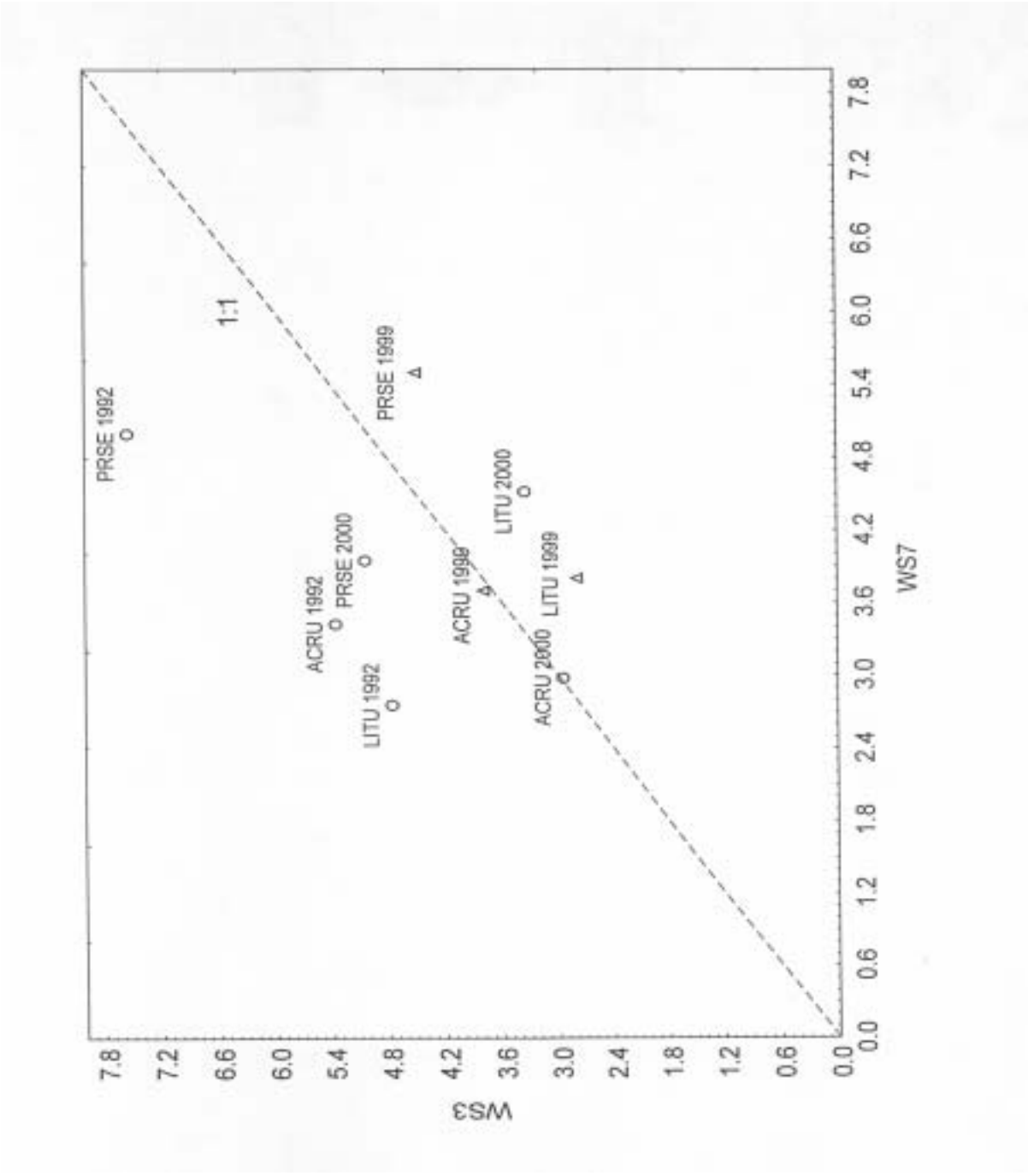

FIGURE 16. FOLIAR N:CA RATIO – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

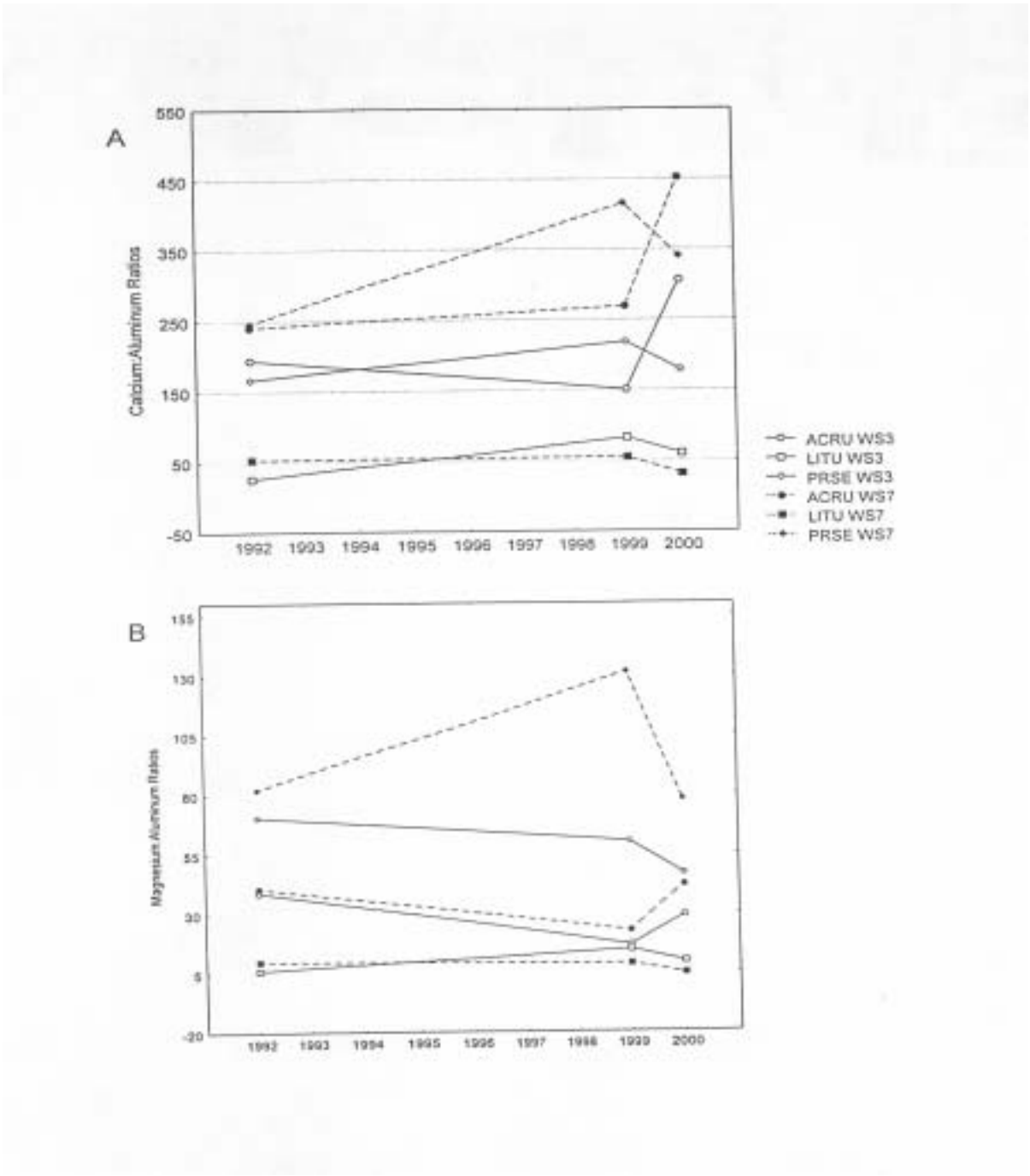

FIGURE 17A. AND 17B. TREND IN FOLIAR CA:AL RATIOS (17A) AND FOLIAR MG:AL RATIOS (17B) FROM 1992 TO 2000 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) ON WS3 AND WS7 AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

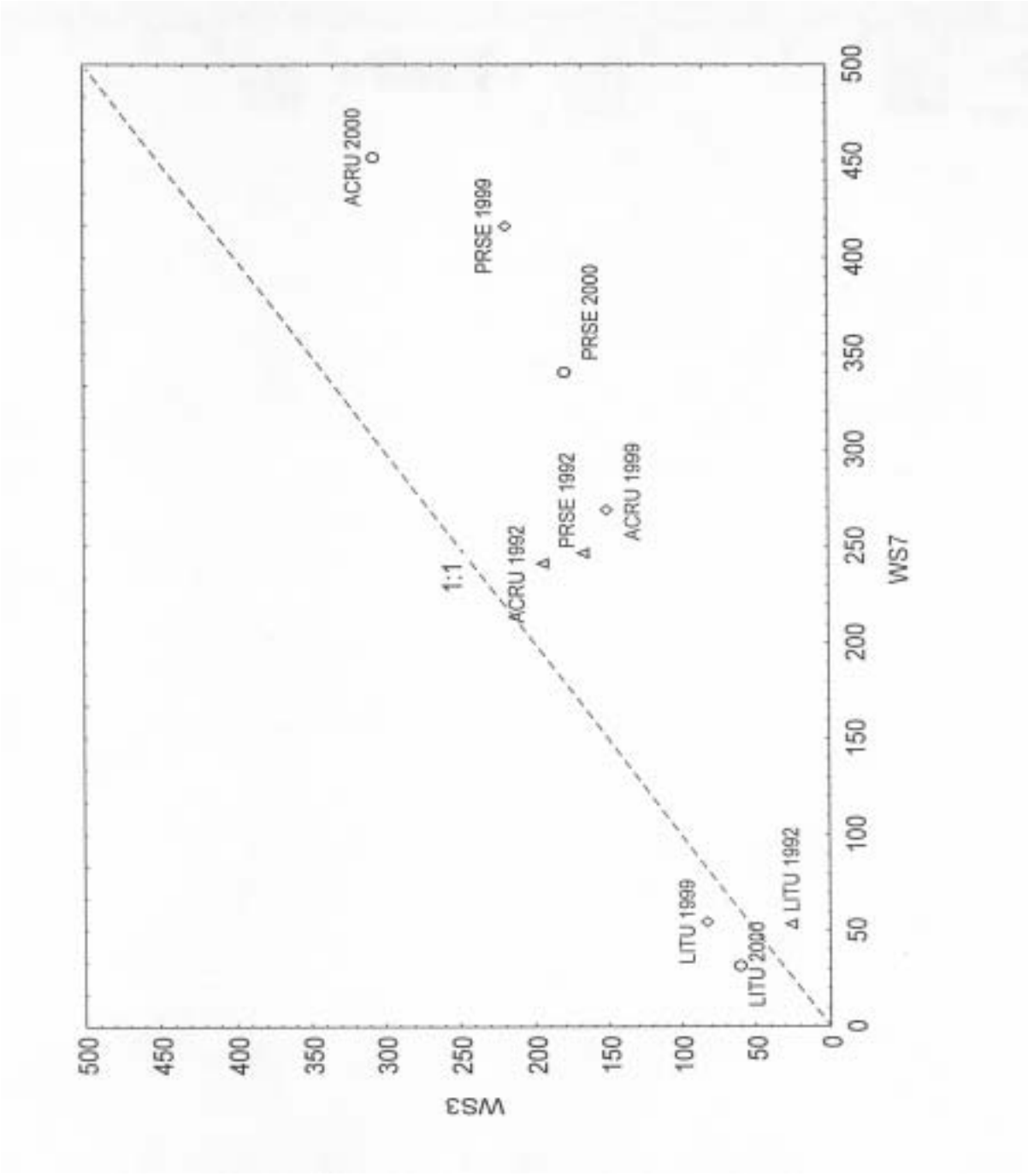

FIGURE 18. FOLIAR CA:AL RATIO – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

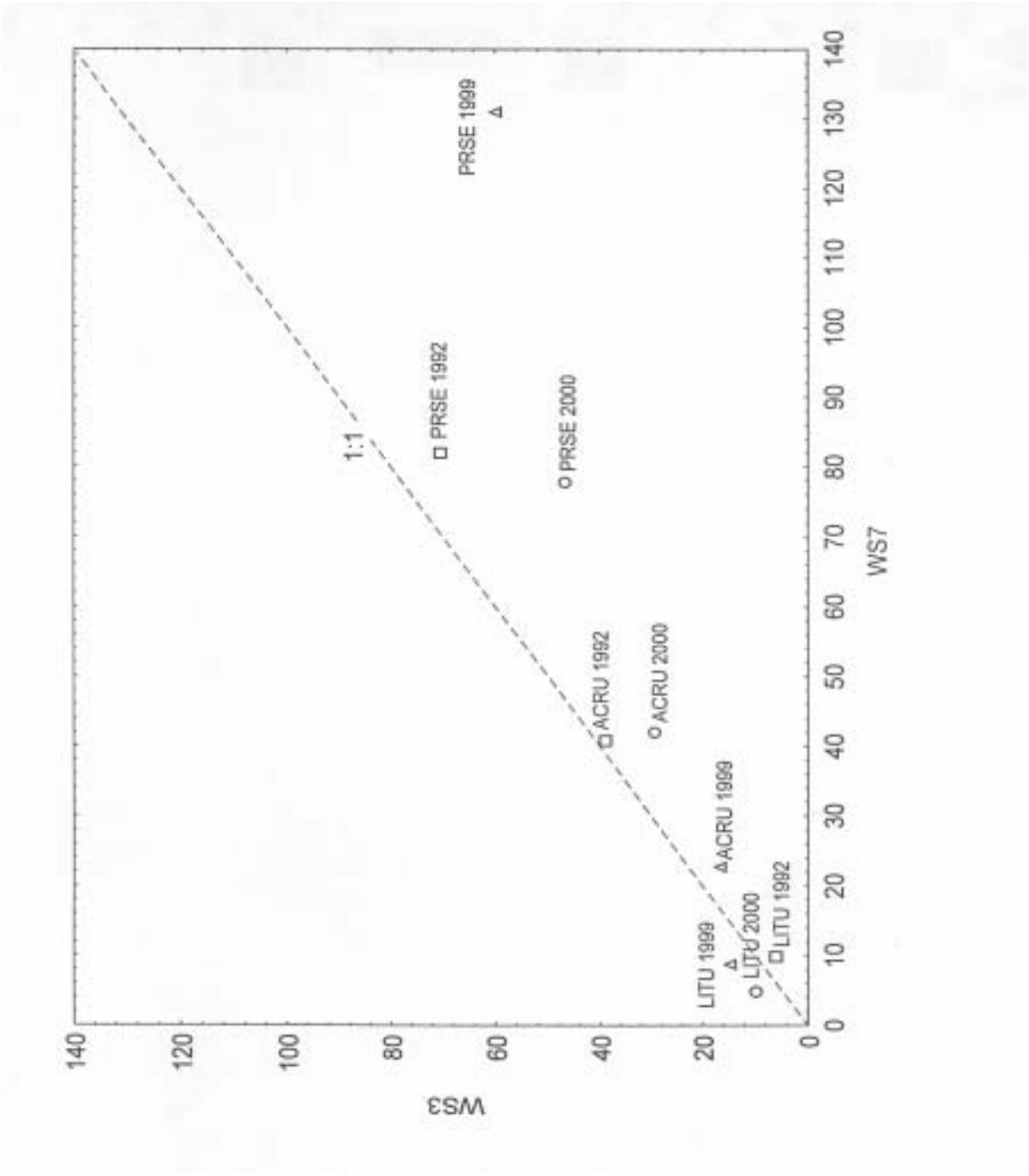

FIGURE 19. FOLIAR MG:AL RATIO – YEARLY COMPARISONS (1992, 1999, AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

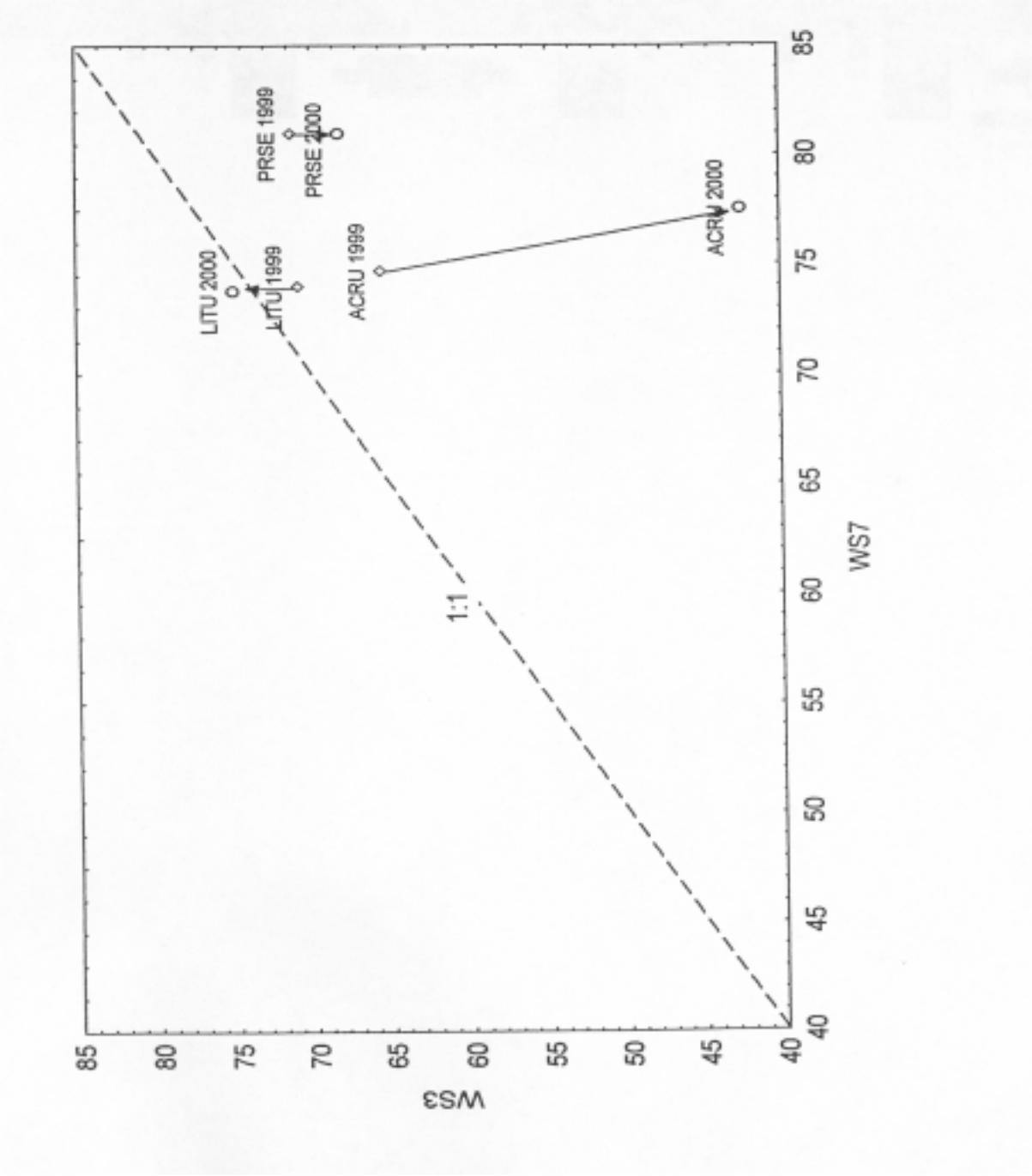

FIGURE 20. NITROGEN RESORPTION EFFICIENCY – YEARLY COMPARISONS (1999 AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

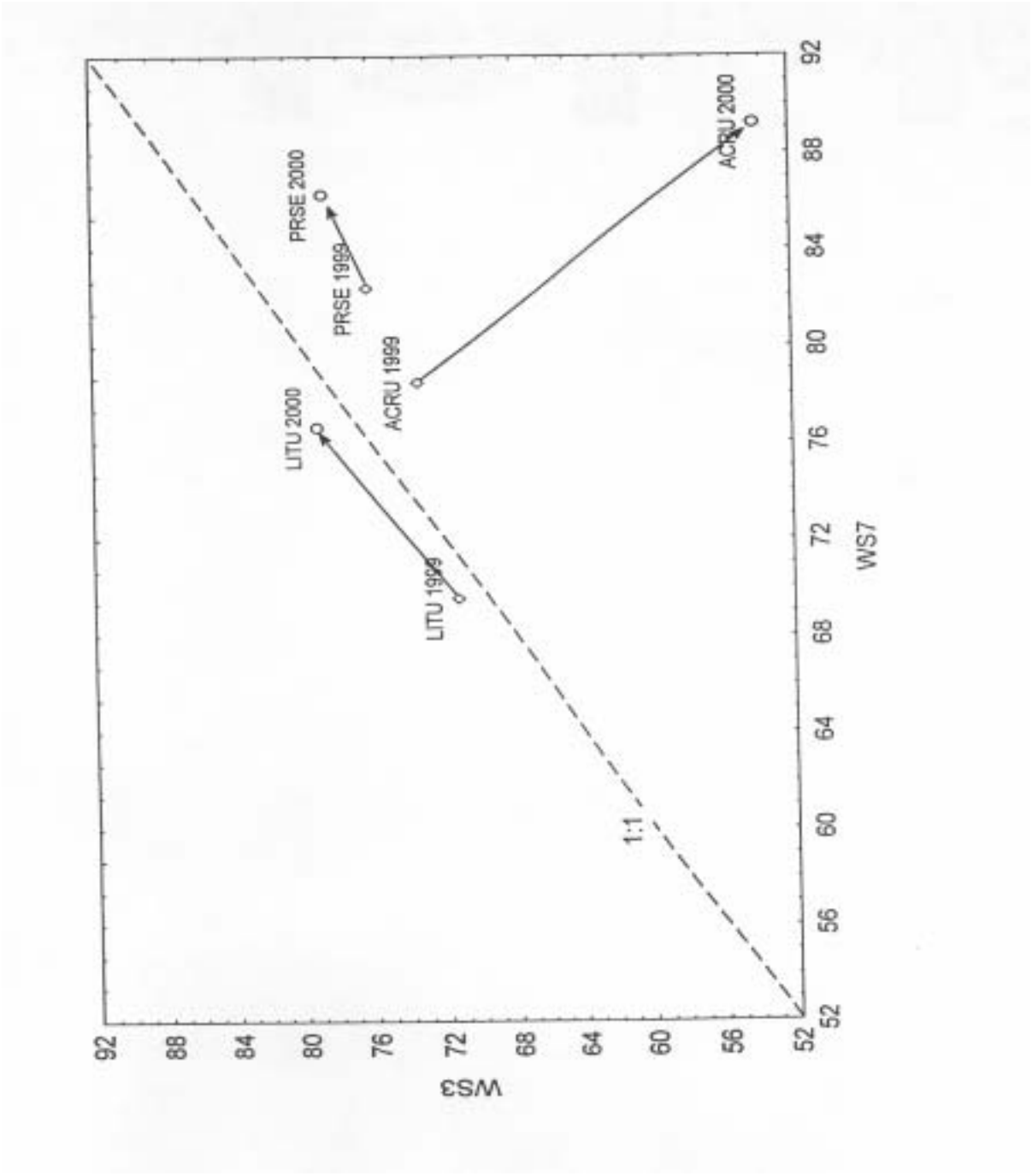

FIGURE 21. PHOSPHORUS RESORPTION EFFICIENCY – YEARLY COMPARISONS (1999 AND 2000) BETWEEN WS3 AND WS7 FOR RED MAPLE (ACRU), TULIP POPLAR (LITU), AND BLACK CHERRY (PRSE) AT THE USDA FERNOW EXPERIMENTAL FOREST, PARSONS, WV (TUCKER CO.).

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